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EXPERIMENTS ON THE BRIGHTNESS VALUE OF RED FOR THE LIGHT-ADAPTED EYE OF THE RABBIT

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I. METHOD

The most fundamental source of error in experiments on color discrimination in animals lies in the possibility that the animals tested, while they discriminate successfully between objects which appear to the human eye of different colors, are in reality seeing the colors as different shades of gray, which would be the case with a color-blind human being. It used to be considered a sufficient precaution against this possibility if the color used were matched with the gray that a color-blind human being would see in its place, and if it were then shown that the animal tested was able to distinguish between the color and its equivalent brightness to the human eye. The work of Yerkes on the dancing mouse¹ and that of Watson on the color-sense of the monkey² have made us realize, however, that the brightness value of a color to the eye of an animal may possibly be quite different from its brightness value to the human eye, so that the animal may successfully discriminate between a color and its equivalent gray to the human eye and still see the color merely as a gray. For the same reason, it is no longer sufficient proof of color vision to show that an animal's choice of a given color is unaffected by such wide variations in its saturation as would to the human color-blind subject cause great differences in the grays seen: though a very dark red and a very light red are equally chosen when presented with a medium green, it is possible that to the eye of the animal even the light red may look darker than the green, so that the discrimination may be based on brightness alone. Evidently, an important step in the investigation of color vision in an animal is to find the brightness equivalent of a given color to the eye of that animal. If it proves to be the

¹ Yerkes, R. M. *The Dancing Mouse*. New York. 1907.

² Watson, J. B. *Some Experiments Bearing Upon Color Vision in Monkeys*. *Jour. Comp. Neur. and Psych.*, vol. 19, pp. 1-28. 1909.

case that the animal tested can learn to discriminate a color, not merely from the gray of equal brightness to the human eye, but from every one of a series of brightnesses ranging from black to white, then we shall have ground for inferring that the color is indeed seen as a color and not as a gray.

Our problem in the present research was to find, if possible, the equivalent brightness for red to the light-adapted eye of the rabbit. We chose red, because the results of Yerkes and Watson have indicated that the brightness value of this color is probably

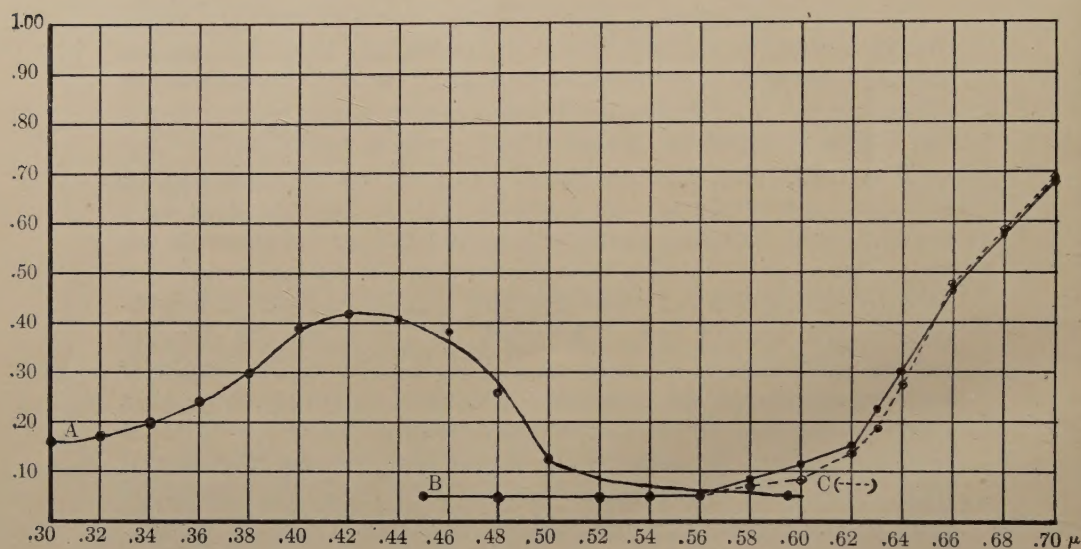


FIGURE 1. Color values of Bradley papers. Curve A, blue; Curve B, red; Curve C, "darkened" red.

different and markedly less for the eye of the dancing mouse and the monkey than for the eye of man. We also made some series of experiments to investigate the brightness value of blue, with less conclusive results.

Our work was done with the Bradley colored papers and the Hering gray papers: we also used a "black" paper supplied by the C. H. Stoelting Company, of a brightness more nearly equivalent to that of Hering gray number 46 than to any of the other Hering papers. While it is desirable that all final work on color discrimination in animals be done with pure spectral colors, yet as the apparatus for the use of such colors as stimuli is compli-

cated and costly, it is, as Yerkes and Watson themselves admit,³ worth while to attempt preliminary work under simpler conditions. Certain sources of error, other than the impurity of the colors, pointed out by Watson as involved in the employment of colored papers, we have, as will be indicated, avoided by slight modifications of our method. Figure 1 shows the reflective power of the colored papers used, measured by means of a MgO screen. Curve A indicates that of the Bradley saturated blue paper; curve B that of the fresh Bradley saturated red paper, and curve C that of the Bradley saturated red paper somewhat darkened by time. The tests of the red paper were made through the kindness of Professor Herbert E. Ives of Cleveland.

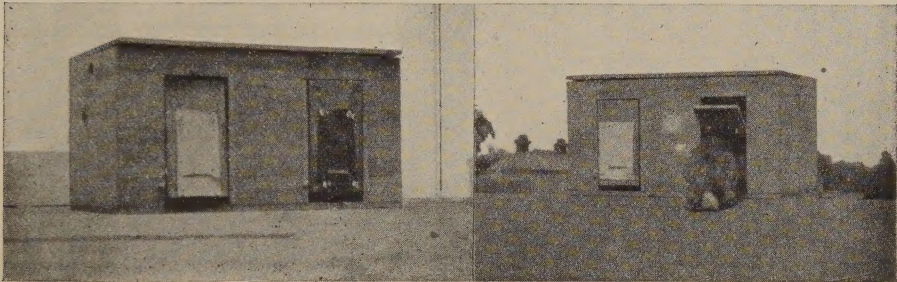


FIGURE 2. Color vision apparatus for testing rabbit. Doors closed.

FIGURE 3. Same, showing rabbit opening door.

Our apparatus consisted of a wooden box, 24 inches long by 13 inches deep and 13 inches high, divided into two equal compartments by an inside partition. Each of these two compartments opened by a door pivoted so as to swing on a horizontal axis; the two doors appeared side by side when the box was viewed from the front. They were 9 inches high by $4\frac{3}{4}$ inches wide. Each door could be fastened on the inside by a button. The lid of the box was hinged so that food could be put in and the doors fastened and unfastened between experiments. On one of the doors was tacked with thumb-tacks a piece of Bradley saturated red paper, somewhat smaller than the door; to the other door was tacked a piece of Hering gray paper of the same size and shape as the red paper. Food was placed in both

³ Yerkes, R. M., and Watson, J. B. *Methods of Studying Vision in Animals. Behavior Monographs*, vol. I, no. 2. 1911.

compartments of the box; but the door carrying the gray paper was fastened on the inside. A rabbit approaching the red door and pushing the lower part of it could get food from the inside; the gray door would not open. The places of the red and gray papers were exchanged in successive experiments (see figures 2 and 3).

One of Watson's objections to the use of colored papers is that if pasted on supports they cannot fail to present inequalities of surface, wrinkles, which will make them easily distinguishable by this means alone. Evidently here, where the papers were not pasted but pinned on the doors in each succeeding experiment, the irregularities of surface could not possibly serve as means of identification, since they were probably different each time the papers were fastened on the doors. Another possibility of error pointed out by Watson as involved in the use of colored papers is that papers of different colors may have differences of surface texture that would render them discriminable even by a color-blind subject. As will be seen, our rabbits proved able to learn the discrimination between red and various grays, but unable to acquire that between red and the black papers used: yet the surface texture of the red paper to ordinary human vision differed more from that of the black papers used than it did from that of the gray papers. A special test of the "texture" possibility of error was made with two of our rabbits. One of them, "Abednego," had made a perfect record in discriminating red and gray number 15 for fifteen consecutive days, eight tests being performed a day. On the sixteenth day pieces of red and grey velvet, matching the papers as closely as possible, were substituted for them. The character of the surfaces here should have been the same, and should have been sufficiently unlike that of the paper surfaces to confuse the rabbit if he had been depending on surface texture. He made a perfect record in the ten tests made, although he seemed much puzzled by the unaccustomed "feel" of the velvet on his nose, and twice *after* touching the red drew back and seemed to look at it. The other rabbit, Polly, gave exactly similar results: an interpolated series of ten velvet experiments did not cause her to make any errors in the discrimination of red and gray number 15.

The *smell* error in its various forms was dealt with as follows. Since food was always, and in equal amounts, in both com-

partments, the animals could not have been guided by the smell of the food in the box. If the same door were open in two successive experiments, the rabbit might be guided by the smell of food on the ground in front of the door, since the food was usually pulled out to be eaten; or by the smell left from previous nosing of the edges of the door. Throughout the greater part of the experiments, however, the open door was on alternate sides in succeeding experiments. Thus the strongest smell of food on the ground or of nosing on the door was regularly on the wrong side; that is, the side that had been the correct side in the preceding experiment. Further, when a given discrimination began to be learned, the correct paper was naturally pushed oftener than the wrong paper; and if the same pieces of paper had been constantly used and shifted from one door to the other, of course the correct piece of paper, which was the red in the experiments with red and greys, would accumulate more of the odor of being nosed than the wrong piece would. Hence we were careful to use a fresh piece of red paper in each test. After the lapse of a few days we used again papers that had been previously employed; from time to time entirely fresh papers were cut, and as we never noticed that the use of perfectly fresh correct papers disturbed the rabbits in the least, we concluded that the odor left by nosing on a paper was not influencing their choice. Again, it is quite conceivable that to a rabbit the different papers used had different intrinsic odors. That this was not a factor of any importance in determining the behavior of our subjects we demonstrated in the following way. After two of the rabbits (Light Nose and Dark Nose) had been in training for twenty-eight days, four tests being given each rabbit a day, a horizontal slit about 5 mm. wide and 10 cm. long was cut in both the red and grey papers at about the level where the rabbit's nose touched them in pushing the doors. Under this slit in the red paper was placed a piece of the grey paper, and *vice versa*. If the animals had been guided by the differing smells of red and grey paper, they must have been somewhat disturbed by an arrangement which brought the grey paper smell in contact with their noses on the red door. The arrangement made no striking change in the appearance of the two doors. Neither of the rabbits was at all influenced by the new state of affairs: both made equally good records before and

after the change. This arrangement of the papers was used in all subsequent experiments with these rabbits: it was used from the beginning in the experiments on three other rabbits (Shadrach, Meshach, and Abednego); and was introduced in a few series with the remaining rabbit (Polly) without producing any change in the percentage of correct choices.

As a routine procedure in all the experiments except the very first ones, where we were habituating the rabbits to the apparatus, we kept out of sight of the animals tested.

It has been stated that our ordinary practice was to have the door which could be opened on opposite sides in successive experiments. It is therefore possible that our rabbits, instead of acquiring a habit based on discrimination between two visual stimuli, were, as their records improved, merely acquiring a habit based on kinaesthetic data, of turning to alternate sides in successive experiments. It may naturally be asked why, in view of this possibility, we did not vary the place of the open door less regularly. Our reason for not doing so at the outset lay primarily in the very strong tendency of the rabbits to form place associations, and to go to the side at which they had last received food. If they were allowed to get food from the same side twice in succession, a tendency to go to this side would be started, and we wished, of course, to force them to depend on visual clues from the first. In our earlier series we were testing two rabbits alternately, and there seemed little antecedent probability that with the comparatively long interval between successive tests with the same animal which this involved, a habit of alternating could be formed. Our later experience showed us, as will appear, that even when the tests followed each other immediately no habit of alternating was formed. The tendency was always rather to go to the side that had been found profitable the last time, and the only exceptions to our practice of alternating the positions of the open door occurred when, to break up a habit of going always to the same side, the open door was kept persistently on the opposite side.

The *motive* leading the animals to push the door, and to acquire an association with one visual impression rather than with the other, was simply the desire of food. The degree of hunger was certainly not constant. The tests were made almost without exception early in the afternoon, between half past one

and half past three. At about nine in the morning the rabbits were given a breakfast of oats. The food used in the tests was always some form of green food, carrots, lettuce, apples, and in season, clover. After the tests were over for the day the rabbits were allowed to eat all the green food they wished. Usually, they seemed to have excellent appetites for the food in the experiment box, but there were variations, and since we had no means of controlling and estimating the strength of our motive, we do not wish to draw any conclusions regarding the speed of the learning process involved. In case of a wrong choice, the only form of punishment involved was sometimes merely the experience of pushing at a door that did not open. More often, the experiment box was removed before the rabbit had had time to go to the other door. But when a new discrimination was being learned, for a short time the rabbit was allowed, after pushing in vain at the wrong door, to go to the correct door and get food. This was occasionally allowed, also, when an animal had made a number of wrong choices in succession and seemed in danger of becoming discouraged.

Another factor which varied in different series, and whose variations would prevent our drawing inferences regarding the speed of the learning process, was the number of tests made on a single animal in a day. In the earlier series only four were made; in some of the later ones eight, ten, or twelve.

A choice was always counted as wrong if the rabbit went near enough to the wrong door to touch it with the long whiskers, for even the lightest touch on a fastened and wholly unyielding door felt quite different from a touch on an unfastened door.

Until the weather became very cold, the two rabbits tested in the autumn of 1910 were kept in a hutch and small yard built for them on the laboratory roof, and the experiment box was placed in this yard for the tests. All the tests with the rabbit used in the fall of 1911 (Polly) were made in this manner. Later in the winter of 1910-1911 the rabbits, except Light Nose, were kept and tested in one of the small rooms of the laboratory, which was brightly lighted by a skylight and a north window. For several hours a day during the winter they were allowed the run of the large laboratory room. During the period when the first series were being made, in the yard attached to the hutch, the two rabbits used as subjects (Light Nose and Dark

Nose) were tested alternately, four tests being made with each on a single day. The rabbit to be tested was admitted to the yard from the hutch door. The experiment box was placed opposite the hutch door, about five feet away from it. As the hutch door was nearer the left side than the middle of the hutch, it was impossible to place the experiment box in such a way that the rabbit should not enter the yard more nearly opposite the left than the right hand door of the experiment box. This fact seemed to have no effect, however, in producing a tendency to push the left hand door oftener than the right hand one. After one rabbit had finished a test, it was driven back into the hutch, and the gravel on the floor of the yard was raked over, to prevent the second rabbit's being guided by the smell of food on the ground where the first rabbit had been eating: the second rabbit was then admitted to the yard for a test. The series made with Polly in the autumn of 1911 were carried on in the same way, except that no other rabbit was being tested at the same time. In the experiments performed in the laboratory room, the rabbit to be tested was taken alone into the room and dropped about three feet in front of the experiment box, which stood on the floor. This method of confronting the animal with the box is not in general to be recommended, as unconsciously the experimenter might give the rabbit an impulse toward one or the other door. But since the results of these series confirmed those obtained under the other circumstances, and since under both conditions the discrimination was acquired in the case of red and grey and not acquired in the case of red and black, no such error seems to have been involved.

II. SUBJECTS.

Our first subjects were two young brown rabbits, a male, Light Nose, and a female, Dark Nose, obtained from a dealer in animals and probably born in captivity, though upon this point the dealer could not enlighten us. Nor did we know their age, but they were neither full grown nor sexually mature. We began our work with these on November 18, 1910. The experiments with the female continued until June 12, 1911, with three interruptions, one of eighteen days during the Christmas recess, one of twelve days due to illness on the animal's part, and one of four days during the spring recess. With these

exceptions she was tested every day. Work with the male lasted until March 12, 1911, at which time we sent him away: he was tested, or at least the attempt was made to test him, every day with the exception of the interval during the Christmas holidays. On January 22 a litter of three males was born (Shadrach, Meshach, and Abednego). Tests on these were begun when they were 24 days old, and were continued with Shadrach and Abednego during the greater part of the time until June 12, 1911. The entire family was disposed of at this date in June. The next fall we obtained from the same dealer a young female (Polly) whose exact age and antecedents were also unknown, and experimented with her from October 3 until December 21, 1911. With the exception of the illness of Dark Nose, above mentioned, all the rabbits remained on the whole in excellent health and spirits during the whole period of work.

As was to be expected, the individual characteristics of the six rabbits differed considerably. Light Nose, the father of the litter was nervous, quick at learning, but decidedly unstable in temperament. After making a perfect record on one day, he would on the next day pay little attention to the box, but frisk about or push the wrong door apparently from a mere vagrant impulse. Dark Nose, the mother, was more stolid and more steady: it was long before she succeeded in making a perfect record, but when a discrimination was once acquired, she maintained a continuous high level of accuracy which her mate never acquired. She showed less tendency than any of the other rabbits to be distracted from the problem in hand, and in working on the difficult discriminations, while she would shake her ears over a mistake, she showed no tendency to delay subsequent trials because of previous failures, but worked with mechanical regularity throughout. The maturing of the sexual instinct in the male put an end to satisfactory work with him. If he was allowed to be in the hutch with his mate at the time of the tests his interest in her overcame his interest in food, and when he was separated from her he was often too restless and ill-tempered to test. For this reason, and because we did not have time to test five rabbits thoroughly each day, we discontinued work with Light Nose in the spring.

Of the three young rabbits, Abednego was most thoroughly tested. He was docile and steady. Shadrach was the most

sluggish and the tameest of the trio. Meshach was an animal with pronounced individuality. He was from birth smaller than the others, and very nervous; until he was about three months old he trembled violently whenever he was picked up. He was also more inclined to show anger by biting, or by thumping with his hind legs on the floor. On one occasion he was accidentally dropped, whereupon he had a kind of convulsion and stiffened out as if dead; he soon recovered, however. When the young rabbits were about two weeks old they were kept in a packing box, the sides of which were fully two feet high. The room in which the box stood was cold, especially at night. One morning Meshach was missing, and was found to have climbed out of the box—a feat which the others did not accomplish for more than a week later,—made his way across the room to the radiator, and established himself in the warmest corner behind it. The most striking instance of the unusual temperament of this small rabbit is found in the behavior which is responsible for the fact that he does not shine in the records. As will be seen, he learned like the others to discriminate red from grey. The other rabbits tested with red and black had found it impossible to distinguish them. As the term drew near a close in the spring, we decided to select one of the rabbits and train it continuously with red and black until the end, so that we might be sure of having given sufficient opportunity for acquiring the discrimination if it could be done. The choice fell upon Meshach. For the first three days he happened to make six or seven right choices out of ten: then came two days in which he went wrong as often as right; and on the next day after this, on being put down before the experiment box, he immediately ran away. Nothing would induce him any longer to push the doors. In the many subsequent trials on that day and on succeeding days, he would thump on the ground with his hind legs, make the peculiar shrill grunt which seems to be the only vocal expression of emotion a rabbit has, and run away on being confronted with the box. His appetite for the food that was given him was as keen as ever, but he never again pushed a door of the box. It seemed odd that a well-formed habit should be so quickly and finally inhibited by an experience of no more poignant unpleasantness than merely pushing at a door which did not open. No pain was involved, for the rabbits seldom pushed hard at a door

which did not at once yield. These tests with red and black had been preceded by seventy experiments with red and grey number 15, in which Meshach had made only eight errors, reacting promptly and readily. While there were other cases where the rabbits took to reacting reluctantly and irregularly, Meshach was the only one who once and for all forsook the habit of opening doors.

Polly, the rabbit tested alone in the fall of 1911, had certain tricks of behavior which distinguished her. She used her fore paws much more than the other rabbits, and if a hand was held out to her would rush at it, grunting, with her mouth open, and paw it violently with her fore paws. She had perhaps been teased before she came into our possession by having food held out to her and withdrawn. She had much less tendency to gnaw objects than the other rabbits had.

Certain peculiarities of behavior were common to all the individuals tested. They all expressed *irritation* by stamping with the hind legs, and when much excited, by a shrill grunting, not very loud, however. The first time we heard this sound it was made by Dark Nose when pursued by her mate. The latter would sometimes make it when he was 'cornered' after he had been running at liberty: sometimes also when he was put down in front of the experiment box after he had attempted to run away. We never heard the rabbits make any sounds to each other, with the exception of Dark Nose's grunts when running away from her mate. There was never the slightest symptom of hostile behavior on the part of the young rabbits to one another: they showed no resentment whatever when their food was stolen from them. The father was never allowed to come near the young rabbits. Expressions of irritation seemed to have no social significance; they were made rather at situations than at other animals. In Dark Nose especially, whose training with the boxes was longest continued, we noted a comical shaking of the ears when she made a mistake. This movement was made occasionally by all the rabbits when they were irritated, as for instance when we were trying to catch them. Very likely its significance as a serviceable associated habit is that it frees the long ears from anything that may be caught upon them. The rabbits occasionally bit our fingers gently when we were holding them; we never saw them bite

one another. The young ones were not sexually mature at the time our work with them ceased: since they were all males it is possible that they might have become more quarrelsome at maturity.

No sounds or movements indicative of *pleasure* were observed, with one exception. Scratching a point on the side of the jaw, under the ear, caused the ear on the same side to droop forward. This movement seemed like a reflex produced by touching a particular spot, yet there were times when it could not be elicited. The rabbits would sit still and allow their noses to be stroked and their ears gently pulled. They never sought these attentions, however.

Little *maternal behavior* was observed on the part of the mother rabbit. She made the usual nest in preparation for the arrival of her offspring, lining a deep hollow in straw with fur from her body. After the young were born we never saw her go near the nest. She manifested no reaction whatever when we took the young ones out, and if we brought her to the neighborhood of the nest she made every effort to get away from it. Probably this behavior is due to a protective instinct to avoid betraying the neighborhood of the nest. When the young ones had emerged from the fur covered nest and were scrambling about, the mother never nosed them, washed them, or paid the slightest attention to them in our presence; they seemed to offer no stimulus to her whatever. Twice we saw a young rabbit come up to her, throw itself on its back and begin to nurse, but on both occasions she moved off at once leaving it sprawling. At no other time did we see her feed them. Despite maternal indifference the litter flourished.

On the whole the rabbits seemed to have little *social behavior*. We never observed them playing together. They would run, jump in the air, and gnaw the floor and woodwork, but they did not chase each other or lie in ambush and startle each other as kittens do: this type of play is evidently characteristic of a hunting rather than a hunted animal. If one rabbit happened to come upon another suddenly it would jump back, but the play would go no farther. They often lay down in little groups, however, and one rabbit would come up to another and offer its face to be washed. The effect was amusing when two of them washed each other's face simultaneously.

This mutual washing seemed their most marked reaction to each other. Corresponding to their lack of social behavior with their own kind was the absence of any such recognition of human beings as a dog or cat would show. Although they were kindly treated and petted, they never seemed to notice us in any way, except that they invariably ran away when approached: no experience could overcome the instinct for flight, probably the strongest instinct a rabbit has. Very likely their lack of eye movements and the fact that, as we shall see, they probably use monocular more than binocular vision, contributed to produce this effect of ignoring us, since it is difficult to judge from its apparent gaze where a rabbit's attention is directed. We never got them to respond in any way to the sound of our voices. They would start at a loud noise, but ordinary noises left them quite unaffected; probably from a protective instinct.

Gnawing, digging in the dirt, running, leaping with all four feet in the air, seemed to be their chief activities. When pursued they almost never ran in a straight line, but displayed the useful instinct of doubling. One instance of an individually acquired habit is interesting. In the small room where the experiments were carried on after cold weather set in there was a box containing earth. Dark Nose happened to jump in this box one day when we were trying to catch her, and allowed herself to be picked up from it and dropped before the experiment box. From that time on, with occasional exceptions, she made a practice of jumping into the earth box between experiments and waiting to be picked up from it and dropped in front of the experiment box. As soon as she had opened the correct door and got food, the experiment box would be removed, whereupon she would immediately run to the dirt box, jump in, and wait, often for several minutes, until the experiment box was ready for the next test, when she would allow herself to be picked up and put before it. Another box containing earth stood in the large laboratory room. When all the rabbits had been tested it was our custom to catch them and put them into the hutch on the roof to spend the night. After the female had formed the habit of jumping into the earth box in the experiment room, she would ordinarily submit to being caught in the large room only when she had jumped into the earth box there.

Her trick of getting into the box and waiting until we were ready to test her proved so saving of our time that we dropped the small rabbits into the same box for safe keeping between experiments with them. After two days of this Abednego formed the habit of jumping in himself, and the other young ones acquired it shortly after. This behavior is interesting when one recalls that Thorndike's cats which had been picked up and dropped into a box never formed the habit of going in themselves⁴: precisely such a connection between being dropped in and jumping in was readily formed by our young rabbits. They would display amusing eagerness for the next test to begin after having jumped into the box, standing on their hind legs and peering over its sides.

It is of course probable that the peculiarities of instinctive behavior which we have described were influenced in a greater or less degree by the domestication of the animals.

III. RESULTS

The plan of our experiments, so far as the arrangement of series is concerned, underwent various modifications in its progress, and therefore will not make upon the reader the impression of ideal order and system. If we could have foreseen these modifications from the outset, there would have been the less need of making the research at all. We shall treat separately the results obtained from each rabbit.

A. *Experiments with Light Nose (male)*

Series 1. Red and Hering grey number 15. Red opens. All of the experiments of this series were performed in the yard attached to the hutch, Light Nose and Dark Nose being tested alternately, as described on page 150. Four tests were made on each day. The rabbits took very kindly to opening the doors, needing only to be shown once or twice that there was food in the box. The *total number of experiments* was 71. The *total percentage of correct choices* made by Light Nose was 63. Calculated at intervals of three days, that is, for every twelve tests, his percentages were 77, 64, 43, 84, 50, 43. It will be seen that his work was irregular, apparently because of playfulness. The series lasted from November 29 to December 16, 1910.

⁴Thorndike, E. L. *Animal Intelligence*. New York. 1911. Pp. 101-2.

Series 2. Red and Hering grey number 7. This was the lightest grey we used in connection with red. Red opens. This series was performed under the same conditions as the preceding one. The *total number of experiments* was 30. The *total percentage of correct choices* made by Light Nose was 84. His percentages calculated for the first three days was 62; for the second three days, 95; for the third two days, 100. The series lasted from January 4, 1911, to January 12.

Series 3. Red and Hering grey number 24 (a darker grey than the others). The conditions were as before. The *total number of experiments* was 73. Light Nose made a *total percentage of right choices* equal to 65. His percentages calculated every three days were 75, 50, 75, 75, 58, 46. His falling off at the end was due to the fact that the presence of his mate was becoming too much of a distraction to him. From this time on we were obliged to separate them. The series lasted from January 13 to January 31, 1911.

Series 4. Red and Stoelting black paper. Red opens. The paper thus designated is that supplied in rolls as black paper by the C. H. Stoelting Company. It varies somewhat in brightness, but stands closer to Hering grey number 46 than to any other of the Hering greys. Light Nose's mate was removed from the hutch and yard during these experiments, and Light Nose was tested alone in the yard. His four tests therefore followed each other at a shorter interval than had previously been the case; and if his previous successes in choosing the red door had been due to a habit of alternating from side to side, this habit should now have had more favorable opportunity to develop. There were 32 experiments in the series. The *total percentage of correct choices* made by Light Nose was 37. The reason why it dropped below 50 was that the rabbit quickly formed the habit of going to the right-hand door in nearly every test. We occasionally tried to break up this habit by putting the red paper on the left-hand door in several successive tests, instead of alternating it from side to side. Fourteen tests were made with the red on the right, in eleven of which the rabbit chose correctly; and eighteen with the red on the left, in which he made only one correct choice. This formation of a place association under conditions which should have strengthened an alternating habit, had one existed, but which substituted a

much darker grey for those previously used, is strong evidence that the rabbits were depending on a visual clue. The series lasted from February 13 to February 20.

Series 5. Red and Hering grey number 7. Red opens. The object of making this series of experiments with the same grey used in Series 2 was to find whether the failure of Light Nose with the red and Stoelting black was due to the difficulty of the discrimination or to some other cause, such as the separation of the rabbits or their physical state. The conditions were as before. Light Nose had by this time, however, become very indifferent to the experiment box. On being admitted to the yard he would commonly sit down and begin a prolonged toilet, at the end of which he would perhaps stroll about the box. When he pushed a door it seemed more the result of a chance impulse than of one based on discrimination. The *total number of tests* was 26; his *total percentage of correct choices* was 65. No place tendency appeared. On the whole, despite the unsatisfactory character of his behavior, some explanation other than indifference seems required to explain the results of Series 4. Series 5 lasted from February 21 to March 1.

Series 6. Red and Hering grey number 15. The conditions were as before. The *total number of experiments* was 29, and the *total percentage of correct choices* was 70. These were the last experiments made with this rabbit, as the work with him consumed too much time. The series lasted from March 2 to March 11.

It will be seen that his percentage of right choices was above 50 in every case except the series where the Stoelting black paper was used.

B. Experiments with Dark Nose (female)

Series 7. Red and Hering grey number 15. Red opens. This series was made with the conditions as described under Series 1, and during the same period. The *total number of experiments* was 71, and the *total percentage of correct choices* made by Dark Nose was 70. Calculated at intervals of three days, that is, for every twelve tests, her percentages were 55, 60, 85, 61, 78, 60.

Series 8. Red and Hering grey number 7. Red opens. Conditions and time as in Series 2. The *total number of experiments*

was 30. The *total percentage of correct choices* made by Dark Nose was 70: her percentage for the first three days was 80, for the second three days 75, and for the remaining two days 66.

Series 9. Red and Hering grey number 24. Red opens. Conditions and time as in Series 3. The *total number of experiments* was 73. The *total percentage of correct choices* made by Dark Nose was 64. Her percentages calculated every three days were 66, 50, 75, 58, 66, 69.

Series 10. Red and Stoelting black paper. Red opens. In the experiments of this series Dark Nose was tested in the small laboratory room, being picked up and dropped in front of the middle of the experiment box, about three feet away from it. Her four tests a day followed each other at a shorter interval than before, when Light Nose was being tested in alternation with her. The same considerations apply with regard to the acquisition of an alternating habit as were noted under Series 4. The *total number of tests* was 58. The *total percentage of correct choices* made by Dark Nose was 31. Like Light Nose, she formed the habit of going to the right-hand door, and we tried to break up this habit by putting the red paper on the left-hand door a number of times in succession. In all, 35 experiments were made with the red on the left hand: in these she chose the red only once. We made 23 tests with the red on the right hand, and in these she chose the red 18 times. The formation of a place association by both Light Nose and Dark Nose when this black paper was substituted for grey is the more noteworthy since the external conditions were now somewhat different for the two rabbits. The series had the same general time limits as Series 4.

Series 11. Red and Hering grey number 7. Red opens. The conditions were as in Series 10. There were 61 tests in the series. Dark Nose made a *total of 80 per cent. of right choices*. In the first half of this series the right-hand tendency persisted: all of the choices were correct when the red was on the right, but only 36 *per cent.* were correct when the red was on the left. In the second half of the series her record was without an error. The series was made between February 21 and March 1.

On March 1 a series of six tests was given in which Stoelting black paper was substituted for red. The black was chosen each time.

Series 12. Red and Hering grey number 15. Red opens. This was the same combination as that used in the first experiments with Dark Nose and Light Nose. The conditions were as in Series 11. A *total* of 36 tests was made in the series, and Dark Nose made but one error, a record of 97 *per cent. correct*.

Series 13. Red and Hering grey number 15, with interpolated red and velvet black tests. On March 11 and 12, after her prolonged and almost errorless record with red and grey number 15, we gave Dark Nose four tests in which for the grey there was substituted the velvety black paper supplied with the Hering color-mixing disks. We were much interested to see her choose the black in all the four trials, wholly neglecting the red which she had been choosing with machine-like regularity. Finding the black door closed, she was allowed to get food from the red door. On the next day four similar trials were given her. The records for this day are in full as follows.

"1. Red on left. Sat still a long time, then went towards red, but swerved and went to black. Box removed.

"2. Red on right. Sat still. Went straight to black, pushed once and ran to red.

"3. Red on left. Very eager to be picked up and put before box. Sat still and seemed to look. Then went straight to red and ate.

"4. Red on right. Sat still a long time. Then went to red door, with a turn of the head towards black, and got food."

On the next five days we proceeded in the following manner. We gave on each day four preliminary tests with red and grey number 15. These were invariably correct choices, without any hesitation on the rabbit's part. Then two tests were given with red and velvet black, and then two final tests with red and grey. These final tests were also always without error. In all there were ten interpolated red and black tests. The results of these may be given in detail from the records.

"1. Red on left. Sat a long time, apparently looking intently, with nose working. Finally started with a jerk, went to black, barely touching it with a whisker. Box removed.

"2. Red on right. Went casually to left side of box, by black; touched black. Box removed.

"3. (Second day). Red on left. Hesitated; went to black. Box removed.

- " 4. Red on right. Went straight to black. Box removed.
- " 5. (Third day). Red on left. Went to black hesitatingly, barely touched it; box removed.
- " 6. Red on right. Went hesitatingly to red.
- " 7. (Fourth day). Went towards black, seemed to look at red, touched black. Box removed⁵.
- " 8. Red on right. Sat a long time facing the box. Finally sauntered to black side and casually touched black. Box removed.
- " 9. (Fifth day.) Red on left. Touches black with nose. Box removed.
- " 10. Red on right. Went straight to red."

Only twice in the ten interpolated red and velvet black tests did the rabbit touch the red, whereas in all the 30 red and grey experiments of the series she went at once to the red. A possible explanation for this may have been that the velvet black looked darker than the red to the rabbit, and that she had acquired the habit of reacting to the darker impression as such, that is, irrespective of the absolute brightnesses involved. This possibility will be considered later. Or, in view of the small number of the red and black tests, the choices of the black may have been accidental.

Series 14. Bradley saturated blue and Hering grey number 7. Blue opens. On the first day 12 experiments were made; on the succeeding days eight each. Otherwise the conditions were as in the immediately preceding series with this rabbit. The *total number of experiments* was 51; the *total percentage of correct choices* was 57. Her percentages for the successive days were 54, 62, 62, 62, 54, 50, 37. On the first day every choice but one was of the left-hand door. On the sixth day every choice but one was of the right-hand door. Various causes might have produced this poor record. The blue might have looked so much like the grey that the rabbit found it difficult to distinguish them; or, if she were capable of acting on the principle of choosing the darker impression as such, and found the blue lighter than the grey, she might have been unable to reverse her habit of choosing the darker; or, finally, the blue might have made upon her a qualitatively new (color?) impression, which she did not have time to learn to associate with food. The one hypothesis made

⁵ See page 151.

unlikely by these results is that in the preceding experiments with red and grey she had been avoiding grey as such rather than choosing red, for continuing to avoid the grey would have produced a perfect record in this series. The series lasted from March 18 to March 24.

Series 15. Blue and Hering grey number 15. Blue opens. The experiments of this series were made at the rate of eight a day. There were 56 in all, and the *total percentage of right choices* was exactly 50. The percentages for each day were 62, 62, 50, 50, 25, 37, 62. Here again the interpretation is doubtful. If the blue were seen as a color, one would have supposed that some signs of an association between it and food should have begun to make their appearance by this time. If on the other hand the habit of choosing the darker impression as such had been formed, and grey number 7 had looked darker than the blue, then even more difficulty should have been experienced in learning to choose blue rather than grey number 15, which is darker than grey number 7. This increased difficulty seems actually to have been felt, judging from the results. The series lasted from March 24 to April 5.

Series 16. Red and grey number 7. Red opens. This series was given merely to re-establish the old red and grey habit in order that it might serve as a basis for some interpolated blue and grey tests. Eight experiments were given a day for five succeeding days: the percentages were 87, 62, 75, 87, 87, 100. The series lasted from April 5 to April 10.

Series 17. Red and grey number 7, with interpolated blue and grey 15 tests. If the grey 15 looked darker than the blue, and the rabbit were capable of forming a habit of reacting to the darker impression in general, then tests where grey 15 and blue were used, interpolated in series where the rabbit was choosing red rather than grey 7, should produce a preponderance of choices of the grey. On each day eight tests with red and grey 7 were given, then a test with blue and grey 15, then a red and grey 7 test, and then a final blue and grey 15 test. In all the 63 red and grey 7 experiments the rabbit went at once to the red. There were altogether 14 of the interpolated blue and grey 15 tests. In these the rabbit touched the grey first 11 times. She did not touch the blue first in any of the six tests made on the first three days. The most obvious explanation of this result is that

grey number 15 looked darker to her than the blue: at the same time the number of experiments is too small to allow us to make this statement with certainty. It is a disadvantage of the method of interpolating tests that much time is required to gather a few results. The series lasted from April 10 to April 16.

Series 18. Stoelting black paper and grey number 7. Grey opens. This series was undertaken with a view to training Dark Nose to choose the lighter rather than the darker of the two papers presented, in order that further color experiments might be made with this reversed habit as a basis. We did not anticipate that it would take as long to form the habit of opening the grey door as proved to be the case. The experiments were made at the rate of ten a day. In all there were 387. The daily percentages of right choices, that is, choices of the grey, were 10, 10, 30, 40, 50, 50, 55, 41, 37, 0, 40, 57, 50, 50, 55, 50, 30, 30, 50, 80, 60, 80, 100, 90, 60, 80, 70, 60, 70, 70, 70, 90, 90, 90, 60, 70. Evidently there existed to be overcome one of two tendencies: either a strong tendency to choose the darker of the two impressions presented, or a strong inhibition of the impulse to push grey, whose absolute character was somehow impressed on the rabbit's mind. The series lasted from April 17 to May 26.

Series 19. Red and Stoelting black paper. Red opens. This series was a final attempt to see whether the red-Stoelting black discrimination could be acquired. Ten experiments were made a day. The total number of experiments was 173, and the total percentage of correct choices was 48. The daily percentages were: 37, 77, 62, 50, 50, 40, 60, 40, 20, 55, 55, 33, 63, 45, 50, 50, 30. Twice in this series a well-marked right-hand tendency appeared and once a left-hand tendency occurred for a short time. Although the red-grey discrimination had been thoroughly learned, and as Series 16 and 17 show could be rapidly re-learned, no progress is shown in learning the red-black discrimination. This series lasted from May 27 to June 12.

C. Experiments with Abednego (male)

The three rabbits born in the laboratory were first tested on the twenty-fourth day of their lives. They were well able to eat lettuce and carrots by this time, and much interested in them. Their slowness in learning the box discrimination seemed

due to the readiness with which they were distracted: their tendency on being put down on the laboratory floor was to wander about aimlessly. They were set down about one foot away from the experiment box, which, to prevent place associations and guidance by the smell of food left on the floor, was moved between experiments. From February 15 to March 11, tests were made on the three rabbits in rotation.

Series 20. Red and Hering grey number 7. Red opens. From February 15 to February 22, three tests a day on each rabbit were made. Abednego had a *total of 45 per cent. of correct choices* in the 33 experiments performed by him. From February 28 to March 11 four tests a day were made on each rabbit. Abednego made a *total of 52 per cent. correct choices* in the 44 experiments performed by him. On the last two days of this part of the series he made a total of *87 per cent.* From March 11 to March 20 the four daily tests on each rabbit were made in immediate succession, that is, the four tests with Abednego were finished before those with Shadrach were begun, and so on. Abednego made a *total of 86 per cent of correct choices* in the 40 tests of this part of the series, and may be considered to have acquired the discrimination.

Series 21. Red and Hering grey number 15. Red opens.

Four tests a day, made in immediate succession, comprised this series. The *total number* of experiments was 96. Abednego made a *total of 77 per cent. of correct choices.*

Three times, on two successive days each time, a right-hand tendency appeared, and on one day every choice was of the left-hand door. The series lasted from April 11 to April 16.

From April 17 to April 23 Abednego was given ten tests daily. In these 60 experiments he made a *total of 95 per cent. of correct choices.*

Series 22. Red and Hering grey number 15, with interpolated red and Stoelting black and red and velvet black tests.

The plan was as follows. Eight tests were given on an experiment day with red and grey number 15, the red opening. Then two tests were made with red and velvet black. Next, two more red and grey tests were given, and finally two with red and Stoelting black. In the red and black tests we tried the experiment of leaving both doors unbolted, so that no punishment was involved for either choice. This was done on the theory

that the rabbit would then make its red and black choices on the basis of the experience gained with red and grey, rather than on the basis of experience gained with the red and black combination itself. Dark Nose had given some indication of seeing the velvet black as darker than the red, and the Stoelting black had apparently been for Light Nose and Dark Nose of equal brightness with the red. If Abednego could be trained to choose the darker impression as such, he should choose the velvet black oftener than the red in these interpolated tests, while no difference should appear in the numbers of choices of red and Stoelting black. The 150 red and grey tests were made without a single error. In all, there were 26 interpolated *red and velvet black* tests. In these he chose the *black* 46 *per cent.* of the time and the *red* 54 *per cent.* There were 31 interpolated *red and Stoelting black* tests: the *red* was chosen 51.5 *per cent.* of the time and the *black* 48.5 *per cent.* of the time. The series offered no evidence that the velvet black was seen as darker than the red. It is possible, though in view of the other results with red and black and of the unlikelihood that the rabbits could accumulate experience from a few experiments of one kind scattered among experiments of a different kind, not at all probable, that the absence of discrimination between red and black was due to the fact that both doors were open in these red and black tests.

A special treatment of the results of the red and black interpolated tests was made to investigate the possibility that the perfect record which the rabbit was making with the red and grey was due to the formation of a habit of going to either side alternately, instead of to a visual discrimination. If such an alternating habit was being followed in the red and grey tests, then when a red and black test was introduced into the series the rabbit should have had a tendency to choose the door on the opposite side to that chosen in the experiment immediately preceding. That such was not the fact is shown by the following figures. Out of a total of 57 interpolated red and black experiments, in 47 *per cent.* the rabbit went to the *same* door that he had opened in the preceding test, and in 53 *per cent.* he went to the *opposite* door. Evidently his perfect series of choices had nothing to do with a tendency to alternate from side to side. The series lasted from April 23 to May 8.

Series 23. Saturated blue and Stoelting black paper. Black opens. The rabbits had been unable to discriminate red from Stoelting black paper, and the only rabbit so far tested with blue and grey 7 and 15 had not learned to discriminate them. The combination of Stoelting black paper and blue paper should then be equivalent, if the black door opened, to the ordinary red-grey combination, the red door opening. Ten tests a day, on May 10 and 11, were given Abednego with the blue and black, and he chose the black without hesitation in each of the twenty tests. Whether the blue looked like grey to him or not, it is probable that the red looked like black.

Series 24. Blue and Hering grey number 15. Blue opens. This was a series of twenty tests only, ten on May 12 and ten on May 13. The blue door was pushed only 30 *per cent.* of the time, seven out of the ten choices on each day being of the grey. It is difficult to account for this sudden tendency to choose the grey, which had not been once touched for a long period, except on the supposition that the rabbit was continuing the habit of choosing the darker impression, and that grey number 15 looked darker to him than blue. One other possibility is that he was avoiding the blue for some reason. But inasmuch as his previous experience with blue had been confined to twenty tests with blue and black, in none of which he had touched the blue, his avoidance could not have been on the basis of experience gained in the experiments. It might have been innate. And the choices of the grey might, in view of the small number of experiments, have been accidental.

Series 25. Blue and Hering grey number 7. Blue opens. This series lasted from May 15 to May 22, a period which included some abnormally hot weather, during which the rabbits were languid and did not work well. There were 76 experiments in all. The *total percentage of correct choices* was 48. The percentages for each day, ten experiments being made on all the days but one, were 40, 30, 70, 60, 60, 33, 50, 50. Unless this record is due to the hot weather, the combination presented great difficulties in the way of discrimination.

Series 26. Blue and Hering grey number 2. Blue opens. This grey is next to the lightest in the Hering series, and to human vision is almost white. The series lasted from May 23 to June 6. One hundred and fifty-four experiments were made

in all. Unfortunately we had reached a period where the young rabbits no longer responded satisfactorily to the tests, whether this was due to the arrival of hot weather or to some other cause. Abednego developed in the course of the series many right-hand and left-hand tendencies. Finally he formed an elaborate habit, which consisted in going to the right end of the box, strolling completely around the box, coming back to the front, and pushing the left-hand door. Sometimes he would turn back on his course before getting all the way around, and then he would push the right-hand door, again the first one he encountered. This habit was broken up by putting the box in a corner of the room, but the rabbit seemed to have lost interest in doors and in the box as a whole, so that we felt little confidence in the results. There were, however, six successive days on which no place tendency appeared, and on these the total percentage of choices of the blue was 63, the percentages of the several days being 50, 70, 70, 80, 60, and 66. There is therefore some indication that blue can be discriminated from grey number 2, either as a color or because it looks darker than the grey.

D. Experiments with Shadrach (male)

Series 27. Red and Hering grey number 7. Red opens. This series was made during the same period as Series 20, and under the conditions described in the report of that series.

In the 33 tests performed at the rate of three a day, the rabbits being tested in rotation, Shadrach made a total of 67 *per cent.* right choices.

In the 44 tests made at the rate of four a day, Shadrach made a total of 61 *per cent.* of right choices.

In the 40 tests made at the rate of four a day, the tests on one rabbit being completed before those on another were begun, Shadrach made a total of 67 *per cent.* of right choices.

No experiments were made on this rabbit from April 16 to May 8. On May 9 and 10 he was given 20 tests, 10 a day, with red and gray number 7, and chose the red every time.

Series 28. Saturated blue and Stoelting black paper. Black opens. This series corresponds to Series 23. Ten experiments were made a day, with the exception of one day on which only six were made. In the 56 tests, Shadrach chose the black 91

per cent. of the time. His results thus confirm, in a longer series, those obtained from Abednego. The series lasted from May 10 to May 16.

Series 29. Saturated blue and grey number 7. Blue opens. This series comprised 287 experiments, made for the most part at the rate of ten a day. His *total percentage of correct choices* for the series was 57. His daily percentages were as follows: 20, 30, 50, 50, 50, 60, 80, 50, 80, 60, 50, 100, 50, 50, 70, 40, 80, 60, 45, 100, 55, 60, 80, 80. It would appear that some progress was being made towards learning this discrimination.

E. Experiments with Meshach (male)

Series 30. Red and Hering grey number 7. Red opens. This series was made during the same period as Series 20 and 27, and under the same conditions.

In the 33 tests made at the rate of three a day, the rabbits being tested in rotation, Meshach made 40 *per cent.* of right choices.

In the 44 tests made at the rate of four a day, Meshach made 47 *per cent.* of correct choices.

In the 40 experiments made at the rate of four a day, without rotation, Meshach made 77 *per cent.* of right choices.

Series 31. Red and Hering grey number 15. Red opens. This series corresponds to Series 21. In the 96 tests of the series, made at the rate of four a day, Meshach made a total of 60 *per cent.* of right choices. His behavior was very irregular, and on two days work with him had to be given up altogether. On the last three days his percentage of correct choices was 58, and on the preceding three days it was 33. The work with this rabbit was interrupted from April 17 to May 8. From May 8 to May 17 he was given ten tests a day, in immediate succession, with red and grey number 15. In the 90 experiments his total percentage of correct choices was 88. Increasing the number of tests a day seemed to steady his otherwise highly erratic behavior toward the experiment box.

The refusal of Meshach to have any further dealings with the box after four days' trial of the red-Stoelting black combination has already been recorded.

F. Experiments on Polly (female)

Series 32. Red and Hering grey number 7. Red opens. These experiments were made in the yard attached to the hutch, under the same conditions as the experiments with Light Nose, that is, the rabbit was admitted to the yard from the hutch for each test, and driven back into the hutch between tests. She learned to run back of her own accord after a test. If any disturbing factor was involved, in the experiments carried on indoors, by the fact that the rabbits were dropped in front of the experiment box, it was absent here and in the work with Light Nose, for these rabbits were usually not touched between tests. The series contained 260 experiments. The daily percentages were as follows: 60, 55, 50, 70, 50, 61, 56, 65, 50, 95, 60, 60, 70, 100, 90, 80, 70, 80, 60, 100, 90, 80, 100, 80, 90.

The series lasted from October 3 to October 29, 1911.

Series 33. Red and Hering grey number 7, with interpolated red and velvet black tests. We wished to see whether this rabbit would confirm the results of Dark Nose in showing a preference for velvet black over red, or those of Abednego in showing no preference between the two. The red door was open and the black door closed in the interpolated tests. Six red and grey tests were given, on an experiment day, in succession; then four red and velvet black tests alternating with red and grey tests. In the 40 red and grey tests the grey was chosen only once. In the 16 interpolated red and velvet black tests the red was chosen 9 times and the black 7 times. There was thus no confirmation of the results obtained from Dark Nose. This series lasted from October 30 to November 2.

Series 34. Red and Hering grey number 15. Red opens. There were 50 experiments in the series, made at the rate of ten a day. The daily percentages were 60, 80, 80, 100, 100. The series lasted from November 3 to November 8.

Series 35. Hering grey number 15 and white. Grey opens. This series comprised ten experiments only; it was interpolated to see whether the rabbit could follow the habit of choosing the darker impression when the absolute brightness of the two impressions was altered. The red was presumably darker than grey number 15, and the rabbit had learned not to push this grey when shown with red. Would she push the same grey when it was shown with white, thus appearing as the darker of

the pair? The white paper used was white letter-paper with a dull finish as nearly like that of the grey paper as we could find. The rabbit chose the grey door in each of the ten tests.

Series 36. Red and Hering grey number 15. Red opens. This series was given to re-establish the habit of choosing red rather than grey. If the rabbit were capable of forming a steady habit of choosing the darker of the two papers presented, irrespective of their absolute brightness, the red-grey discrimination would not need to be re-established after the grey-white series, since in both sets of experiments the darker paper was the one to be chosen. As a matter of fact the red-grey discrimination was not so good after the grey-white series had been made as it had been immediately before. Ten experiments a day for three days, November 10, 11, and 12, were made, the percentages of choices of the red being 80, 70, and 80.

Series 37. Tests with red and grey number 15, the red open, intermingled with tests with grey number 15 and white, the grey opening. This series followed a new plan. Twelve experiments were usually given on a day. Six of them were red and grey 15 tests, the other six were grey 15 and white tests. Two of a kind were usually given in succession, the open door being on opposite sides in the two. The grey door was closed if shown with red, open if shown with white. The open door, though on opposite sides in the two succeeding tests of the same kind, was sometimes in the next following test on the same side as in the one immediately preceding, and sometimes on the opposite side: that is, the alternation of the sides on which the open door was to be found was not continued through the whole series.

The total number of *red and grey* experiments was 77; in 73 *per cent.* of these the *red* was chosen. The total number of *grey and white* experiments was 70; in 72.8 *per cent.* of these the *grey* was chosen. The percentages calculated every three days, that is, for (usually) every 18 tests of each kind, were as follows: choices of the red in red-grey tests, 74, 73, 68, 76; choices of the grey in grey-white tests, 73, 78, 86, 52. On one day, November 20, a perfect record was obtained in the whole twelve experiments.

It does not seem possible to explain the high percentages of choices of the grey in the grey-white tests, the very same grey which the rabbit had learned to avoid in the red-grey tests,

except on the supposition that to a certain extent a habit had been formed of pushing the door which carried the darker paper, irrespective of the absolute brightnesses involved. Yet the absolute brightnesses were apparently not wholly without effect. In the latter part of this combined series the rabbit began to show signs of confusion. Further, as has just been noted, if the habit of reacting to the darker impression as such had been perfectly formed, the introduction of grey-white tests ought not to have had an unfavorable effect on succeeding red-grey tests. That such an effect probably was exerted is shown by the results of the next series. Series 37 lasted from November 13 to November 24.

Series 38. Red and grey number 15. Red opens. This series lasted from November 25 to December 6. There were 105 experiments in the series, made, with the exception of one day, at the rate of ten a day. The *total percentage of correct choices* was 62. The percentages on successive days were 60, 90, 30, 60, 70, 35, 80, 70, 56, 80. The rabbit's behavior suggested that the difficulty lay in the fact that the grey, whose absolute character was somehow recognized, sometimes set off the impulse to push it, as in the grey-white tests of the preceding series, and sometimes inhibited the impulse, as usually in the red-grey series. When the animal started in the direction of the red, she ran to it and pushed without hesitation; when she started for the grey she commonly drew back or stopped on the way to it, either finally pushing it after doing so, or turning to the other side and pushing the red.

Series 39. Red and Hering grey number 46. Red opens. The paper called "Stoelting black" in preceding series was, as has been said, nearer in brightness to Hering grey number 46 than to any other of the Hering greys. This last series was undertaken to find whether Polly, working with red and grey number 46, would get results like those obtained by Dark Nose, Light Nose, and Abednego in their experiments with red and Stoelting black paper. There were 180 tests in the series, twelve experiments being made on a day. The series lasted from December 7 to December 22. The *total percentage of correct choices* was 52. The daily percentages were 58, 58, 58, 58, 50, 58, 50, 58, 66, 50, 50, 66, 42, 50, 66. This series of figures may fairly be compared with those from Series 32, with red and grey number

7. Although Series 32 was the first which Polly made, and involved getting acquainted with the apparatus and the situation in general, she had made decided progress towards learning the discrimination at the end of 180 tests: her percentages for the first eighteen days were 60, 55, 50, 70, 50, 61, 56, 65, 50, 95, 60, 60, 70, 100, 90, 80, 70, 80.

It may therefore be concluded that like the other rabbits tested, she found it impossible, in the time allowed, to learn to distinguish between red and a grey of the brightness of Hering grey number 46, that is, a grey dark enough to be called black.

Supplementary tests on binocular vision

The rabbit has a small field of binocular vision, if we judge by the angle through which both eyes can be seen at the same time, a test which Waugh has applied to the mouse. In order to get some light on the question as to how much use the rabbit makes of binocular vision as compared with monocular vision, we made some simple tests on Polly. When she was sitting still, two bits of lettuce of equal size were held out, one straight in front of her nose at a distance of three or four inches, the other in line at right angles, directly in front of her left or right eye, and at an equal distance. Out of fifty trials the rabbit only twice took the bit of food held in front. The other forty-eight times, after sitting motionless a few seconds, she turned her head to the side and took the food offered there. It would appear that her actions were determined rather by monocular than by binocular vision. The rabbits seemed from our general observation of them to be influenced by binocular vision to a certain extent in their movements: that is, they seemed to avoid by vision objects directly in front of them. We often noticed in the box experiments, however, that a rabbit would turn its head from side to side before making a choice: sometimes a record like the following would be made: "Rabbit starts towards red, stops, looks at grey, turns back to red and pushes it." The experiments on Polly, just described, indicate that when a rabbit turned its head so as to face one of the doors, it was really looking, monocularly, at the other door. Thus the looking at grey described in the record was probably merely a turning of the head so as to get a better, that is, a monocular, view of the red before pushing it. And in

turning the head from side to side, the rabbit is really looking at the object *from* which its face is turned.

IV. CONCLUSIONS

1. The rabbit can discriminate Bradley saturated red paper from Hering grey number 7 (Series, 2, 5, 8, 11, 16, 17, 20, 27, 30, 32, 33); from Hering grey number 15 (Series 1, 6, 7, 12, 13, 21, 22, 31, 34, 36, 37, 38), and from Hering grey number 24, though few tests were made with this grey (Series 3 and 9).

2. That this discrimination is a true visual discrimination and not one based on smell or some other clue; further, that it is based on brightness rather than on color difference, the red being seen as darker than the grey, is indicated by the fact that the rabbits gave no evidence of ability to discriminate red from "Stoelting black" paper or from the very dark Hering grey number 46 (Series 4, 10, 19, 22, 39), while the ability to discriminate was again shown as soon as a lighter grey was used (Series 5, 7, 22).

3. One short series (Series 13) suggested that Hering velvet black looks darker to the rabbit than Bradley saturated red. Series 22 and 33 failed to confirm this, and gave no evidence that red was discriminated from Hering velvet black paper.

4. Red has a very low stimulating effect on the rabbit's retina; a result which corresponds to what Yerkes has found for the dancing mouse and Watson for the monkey. Our experiments furnish no evidence that red is seen as a color: on the other hand they do not prove that it is not so seen. The rabbits may simply have found it impossible during the period of the training to base discriminations on color rather than on brightness differences. Whether color difference exists or not, the rabbit evidently attends more readily to a brightness than to a color difference.

5. The results regarding the brightness value of saturated blue are not conclusive. It seems to be readily distinguished from "Stoelting black" paper (Series 23 and 28), a discrimination which may be based either on brightness or on color difference. That the difference involved is mainly one of brightness, the blue looking lighter than the black, is indicated by the fact that blue and grey 7 were not discriminated in the course of 51 experiments by Dark Nose (Series 14), nor in the course

of 76 experiments by Abednego (Series 25). There is some evidence that grey number 15 looks darker than saturated blue: Dark Nose showed a marked tendency to choose grey 15 rather than blue in tests interpolated among red and grey tests where she was choosing the red, that is, the darker impression (Series 17); Abednego showed a tendency to choose grey 15 rather than blue in a series of 20 experiments following on a long experience of choosing the darker impression (Series 24). There was some evidence that saturated blue can be discriminated from the very light, almost white, Hering grey number 2, whether through brightness or color difference (Series 26). On the whole, it is suggested by our results that the brightness equivalent of saturated blue is in the neighborhood of Hering grey number 7, that is, decidedly lighter than would be the case for the human eye. It is interesting to note that one of Breed's chicks, which preferred white to black and yellow to black, preferred Bradley saturated blue to a yellow which was "very light, much brighter than the comparatively dark blue, not only as judged directly by the human eye, but as tested by the flicker method."⁶

On the other hand, the rabbit Shadrach, in next to the longest single series of tests made, showed some evidence that he was learning to discriminate saturated blue from grey number 7 (Series 29). If the discrimination was being acquired, it may have been based on a very slight brightness difference, or on a color difference.

6. When discrimination became difficult for the rabbits they fell back upon a habit of always choosing the door on one side of the box. Out of 39 instances where such a habit was recorded, it was a left-hand habit in 9 cases only, and in all these left-hand cases the habit persisted for one day only, while a right-hand habit often appeared for several successive days.

7. The rabbits did not acquire a habit, based on kinaesthetic data, of alternating from side to side in their choices, but were throughout guided by visual clues. This is shown by several facts.

a) No matter how regularly they had been choosing red in red-grey series where the red was on either side alternately, the red habit immediately broke down when black was substituted

⁶ Breed, F. S. The Development of Certain Instincts and Habits in Chicks. *Behavior Monographs*, vol. I, no. 1. 1911.

for the red. This was especially striking in Series 4 and 10, where, when the red and black tests were begun, the interval between successive tests on the same animal was greatly reduced, a circumstance which should have strengthened a motor habit of alternating from side to side, whereas in fact the alternation which had occurred while red and grey were being used now gave way to a habit of choosing the door on one side only.

b) When in the midst of red and grey series in which red was being regularly chosen as it occurred on alternate sides, single tests were interpolated where black was substituted for grey, the tendency to choose the door on the same side as the one chosen in the preceding test was about as strong as the tendency to choose the door on the opposite side (Series 22).

c) In series where a high percentage of correct choices was being made the rabbits would often move first in the direction of the wrong door, checking themselves while a foot or more away and turning to the correct door. This would hardly have been the case had a motor habit been formed.

8. The results were not based merely on the formation of an inhibition of the impulse to push the grey door. Breed, in his work on chicks, found evidence that in color tests they were not so much learning to choose one door as to avoid the other. Thus, after they had learned to choose black instead of blue, they chose white instead of blue, indicating that the discrimination was not based on a brightness difference, but rather on an acquired avoidance of blue.⁷ Is it possible to explain our results with red by supposing that the rabbits learned in the red-grey experiments to avoid grey, rather than to choose red as the darker impression, and that they failed in the red-black tests because the grey, to which they had learned to check reaction, was no longer before them, so that their impulses were equally divided between the two doors which they saw? Undoubtedly the learning did involve the acquired inhibition of an impulse to push the wrong door: not infrequently, as we have said, the rabbit would run to within a short distance of the wrong door, stop abruptly, and turn to the other one. At other times, for long periods, the animal would dash at once to the right door as if the sight of it set off the impulse instantly. A careful examination of our results shows that the difference

⁷ *Op. cit.*

between the figures for red and grey and those for red and black cannot be due simply to the absence of grey in the red-black experiments. In Series 19, Dark Nose was required to learn to choose red rather than Stoelting black paper. She had previously been trained to choose grey number 7 rather than Stoelting black. This training, which had been continued for 387 experiments, had resulted in an average of 75 per cent of right choices in the last 180 tests. On the theory that the rabbits were learning to avoid the wrong door in itself, rather than to choose the darker or lighter of the two impressions presented, this black-grey training should have brought about a certain tendency to avoid the black, and inasmuch as, in the next series, with red and black, the red door opened, the rabbit ought to have continued to make a high record of correct choices, since all that was necessary was to continue to avoid the black. But we find that her total percentage of correct choices in this black-red series, comprising 173 experiments, was only 48. It is difficult to explain this failure to continue the process of learning to avoid black, except on the supposition that the rabbit found it practically impossible to distinguish red from black. The details of her behavior for the first three days of this black-red test are interesting. In the preceding series she had been going for the most part without hesitation to grey, though occasionally making a wrong choice. Our records read as follows for the first day of the final red-black series.

"1. Red left. Put down before the box, rabbit runs away. Start over again. She goes near red, looks at it, goes around to left end of box and sits down. Start again. She noses red and black alternately. Gets food from red.

"2. Red right. Looks intently, goes to black [which she should have been learning to avoid], barely touches it, cautiously pushes red.

"3. Red left. Goes to middle, pushes red, shaking ears.

"4. Red right. Looks at box, dashes off to left, noses black, then red.

"5. Two trials, but rabbit runs away each time."

The next day's work led off with six successive choices of the red. Two choices of the black follow, and then two more of the red. It looked as though there might have been here some recognition either of the red as the door to be chosen, or of the

black as the door to be avoided. But on the next day the records read as follows.

- " 1. Red left. Towards red, pause, pushes red.
- " 2. Red right. Red.
- " 3. Red left. To black, pushes, shakes ears, to red.
- " 4. Red right. To middle, to red.
- " 5. Red left. Starts towards red, turns and faces black, stretches so that whiskers just touch black, shakes ears, pushes red.
- " 6. Red right. Touches black, to red.
- " 7. Red left. Went to left side, then to red.
- " 8. Red right. Went towards red, pauses a long time, finally pushes."

And in the ten experiments performed the next day she chose the right hand door every time, although with much hesitation and ear-shaking. There was no evidence from this time on in the series that red and black were distinguished.

As further proof that something more than an acquired avoidance of a particular visual impression *as such* is involved in our experiments, we may take the behavior of Dark Nose in Series 17. Here she was given daily 9 tests for seven days with red and grey number 7, in which she never failed to choose the red. In each day's series there were interpolated two tests with blue and grey number 15, and in these 14 experiments the rabbit touched the grey first 11 times. This does not look as though she had been avoiding the grey *as such* in the grey-red tests. It is true that the same grey was not used in the red-grey and blue grey experiments, but if we are to explain all our red-gray series on the supposition that they involved avoidance of grey *as such*, we must suppose that experience with one grey was transferred to the other greys, for Series 2 and 8, with red and grey number 7, gave high percentages of correct choices which could be accounted for only by supposing them due to the experience gained in Series 1 and 7: either the rabbits had there learned to choose the darker impression, or to choose the red *as such*, or to avoid grey, whether number 7 or number 15, *as such*.

Again, Abednego, after long training to choose red rather than grey, was offered the choice between blue and black, and invariably chose black (Series 23). If his preceding training had taught

him simply to avoid grey as such, we should explain this behavior by saying that blue looked like grey to him here. But in the next series he was given blue and the grey (15) with which he had had most preliminary training, and he chose the grey 70 per cent. of the time.

On the whole, then, the consideration of the possibility suggested by Breed's work does not require us to modify our conclusions. Doubtless the reason why positive avoidance of a given impression as such plays more part in his experiments than in ours is that he used a much stronger punishment for wrong choices than we did; his chicks were given electric shocks, while our rabbits merely pushed against closed doors.

9. To a certain degree, the rabbit is able to form a habit of choosing the darker of two impressions, irrespective of their absolute brightness. It has been noted that we have found such a supposition useful in explaining, at several points, the behavior of our rabbits in a new series as due to their experience in previous series. No other hypothesis seems conceivable to explain the results of Series 37, where Polly chose grey 15 72.8 per cent of the time when it was presented with white, and only 27 per cent. of the time when it was presented with red. But the rabbit has no grasp such as human beings would gain of the *principle* of choosing the darker impression: the absolute brightnesses involved have a disturbing influence, as suggested by the fact that ordinary red-grey series, presented after the complex series, (Series 38 after 37), and after a short grey-white series (Series 36 after 35) showed a falling off in the percentage of correct choices, apparently due to the association of conflicting impulses with the grey as such.

10. There is evidence to indicate that while probably capable of binocular vision, the rabbit uses monocular vision in preference.

MAGNETIC CONTROL OF GEOTROPISM IN PARAMOECIUM

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In a preliminary paper the writer showed that cultures of *Paramoecium caudatum* which have ingested iron particles show an increased negative geotropic response for a temporary period. It was observed that the particles are at first lodged in the posterior end, and that the changed response is coincident with this condition and tends to disappear as the particles become more evenly distributed through the endoplasm. In an animal so loaded the posterior end tends to sink more rapidly so as to cause it to assume an upward orientation, provided that it is moving in a narrow spiral or nearly straight path, i. e., in the absence of any marked deflections of the anterior end such as occur when the animal is stimulated. This is readily observed, particularly in individuals which start to move in a horizontal direction. The action is to be interpreted as a passive orientation to gravity not involving response to a stimulus.

This result naturally suggests the possibility of experimenting with the magnetic control of the movements of *Paramoecia* containing iron. In this paper follow some experiments with the combined effects of gravity and magnetism.

APPARATUS AND METHODS

An electro-magnet was employed wrapped for a length of 27.5 cm. with seven turns of wire, 57 turns to the cm. The core was of ten pieces of a diam. of 4.5 mm., 31 cm. in length. An alternating current from the lighting circuit was used, which was passed through a 50 w. incandescent lamp in series. A direct battery current was also tried for comparison, but its use gave no different results.

A half-gram or so of iron by alcohol is rubbed up fine in an agate mortar with a few drops of water. From 1-2 cc. of water containing a dense culture of *Paramoecia*, free from sediment, is added and the iron kept in suspension by drawing the water in

and out with a pipette; or the whole may be placed in a small vial and turned back and forth. After this treatment the Paramoecia may be recovered without the iron by pouring the whole into a Syracuse watch glass with water and the Paramoecia removed with a pipette by several rinsings. They were then placed for experimentation in a flat rectangular jar about $3 \times 1\frac{1}{2} \times \frac{3}{4}$ inches. This was supported with its narrow face against the core of the magnet. The water used is preferably boiled to drive away gases. The normal geotropic reaction of Paramoecium, as Jennings points out, is a delicate one and is best elicited in pure water in the absence of disturbing chemical factors and mechanical agitation. But as pointed out in the previous paper ingestion of iron accentuates the geotropic response so that it is not so readily masked by chemical and other factors.

EXPERIMENTS

1. *Ingestion of iron for a relatively long period, five minutes or more.*

Three controls are needed in connection with this experiment. First a culture of normal Paramoecia in a similar vessel and subjected to similar shaking, as mechanical agitation has a tendency to drive them to the bottom. The control Paramoecia used in this set of experiments were taken from a dense ring round the edge of the water in the stock jar. They showed a slight normal upward tendency after a time, but were apt to remain rather evenly diffused and finally to settle all over the walls of the jar, which was probably due to the large extent of its inner surface. Other cultures sometimes display a tendency to go downward or more commonly aggregate toward the top and occasionally form a ring.

As a second control such a jar of Paramoecia may be brought into the field of the magnet, which gave no effect, and would disprove the existence of anything in the field itself to influence the movements.

Specimens of the treated culture under the microscope showed a heavy load of iron particles. The behavior of such a culture without the magnet furnishes the third control experiment. These moved downward and soon left the upper third of the jar fairly free from Paramoecia. A considerable number would come to rest on the bottom where they would remain for short

intervals before rising. After the lapse of a half hour, more or less, such a culture as this aggregates rather densely toward the bottom, presumably as a result of ciliary fatigue. After 24 hours, or even less, they may all be found risen again and apparently no worse for the treatment.

When such a treated culture is placed in the field of the magnet, as soon as the current is turned on there begins a strong upward streaming past the pole and as a result a downward movement also becomes manifest on the side away from the magnet. The downward movement is wider and more diffuse than the upward. The latter was a narrow stream up to a half inch in width. The concentration of this upward streaming gives it a striking appearance, while the downward movement is more scattered. Thus the culture shows the decided appearance of being in a state of circulation. Some of the *Paramoecia* in the upward stream continue on up to the surface of the water, but more usually they begin to disperse in all directions. They may move to a short distance, meanwhile sinking, and return to the upward stream, or they may go farther away before they finally sink. A considerable aggregation is found in the outside lower corner, i. e., away from the magnet.

As to the explanation of the upward streaming, it is evident that it involves explaining the upward orientation of the animals and their ability to rise in the stronger part of the magnetic field, while elsewhere they tend to sink. It is apparent that the movement upward arises mainly from below the pole and also from the side, and that it consists chiefly of upwardly oriented animals which do not congregate at the pole, but rather move more freely the nearer they are in its vicinity, and frequently keep on going upward. They appear therefore to experience a greater buoyancy in the magnetic field, so that we may assume the effect of the magnet to be due to its diminishing the effect of gravity upon the heavily loaded animals. Their upward orientation is another matter and is explicable by gravity alone, based on the observation that the posterior end is of higher specific gravity than the anterior where the stronger cilia are located.

To better understand this we need to refer to Jennings' lucid description of the action system of the animal. When *Paramoecium* is unimpeded in its progress in any way it tends to

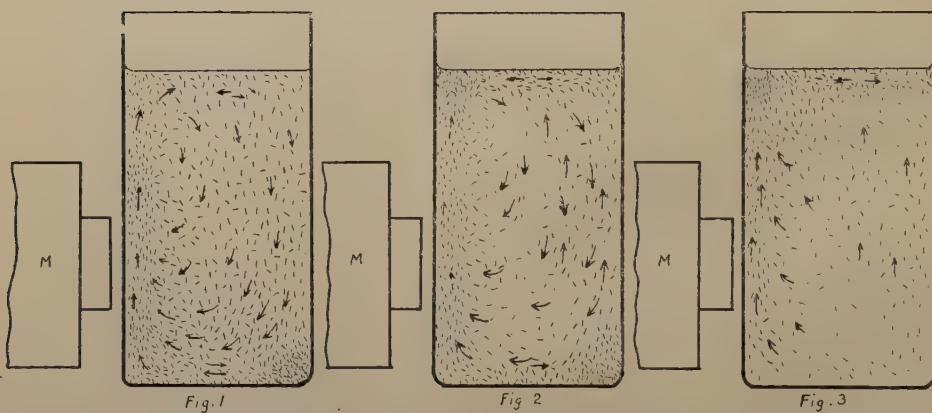
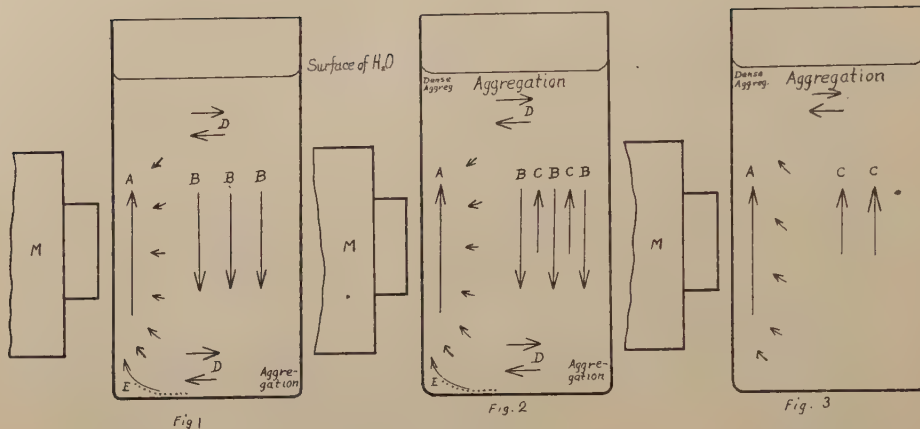


PLATE I. Figures 1, 2, 3, refer to experiments in the text of the same number.

The arrows indicate the oriented movements upward, downward, and toward the magnet.

► Random movements of dispersal from the top of the upward stream, and at all other points, are not represented.

A, upward oriented movements in the region of increased buoyancy.

B, heavily loaded animals moving downward in the weaker magnetic field.

C, upward oriented animals consisting presumably of those which are less heavily loaded. These tend to form the aggregation at the top which appears in (2) and (3), but not in (1).

D, horizontal paths of animals very close to the water surface or to the bottom, which appear to be governed by nearness to these surfaces.

E, individuals lying quiescent on the bottom, drawn passively at first toward the magnet.

The small curved arrows represent paths toward the magnet. The animals swing gradually into the upward stream. The arrows are curved to indicate this fact. Plate 2 illustrates the same facts by another method.

move in a very narrow spiral or nearly straight path. In this condition it is easy to observe that the tendency of the posterior end to sink and bring the animal into a position of vertical equilibrium with anterior end up is of very great effectiveness. On the other hand when the animal is stimulated externally in any way the swerving habit entirely annuls the passive sinking tendency of the posterior end and becomes the chief means of orientation. The anterior end can orientate the animal actively, the posterior end only passively. Now when a heavily loaded *Paramoecium* moves upward outside of the region of increased buoyancy, it meets with just such a difficulty in its movements as will cause it to swerve in a broad spiral and until the changed path is downward it will continue to move in that sort of a spiral, which, as Jennings shows, is highly adaptive for bringing the animal into a new direction where the stimulus to change will be lacking.

The movement toward the magnet is the most diffuse feature of the circulation, so that superficially it might be set down as the result of the random movements of the animals. Ocular demonstration of the existence of a definite orientation toward the magnet is apparently rendered difficult for two reasons. First, orientation toward the magnet is accompanied by a gradual orientation into the vertical position of equilibrium by sinking of the posterior end, so that the actual path traversed is a curve. The animals do not appear moving in parallel lines, which is quite a striking feature of the upward streaming. Second, there are two paths of less resistance, toward the earth and toward the magnet and considerable intermingling of the two effects. Evidence of a direct pull of the magnet is best seen upon those animals which may be lying quiescent upon the bottom just within its influence. These often appear to move at first as if dragged like passive objects.

The remaining feature of the circulation to be considered is the dispersion of the animals after they cease to go upward in the field of the magnet. At some point, which differs with different individuals, they begin to swerve and disperse horizontally. The further they move away, of course, the more likely they are to be influenced by gravity more than the magnet and return to the bottom.

2. *Ingestion of iron for a moderate period, two minutes.*

In such a culture as this it was found that a large number of the animals in a control orient upward and aggregate toward the top of the water. But a considerable number showed evidence of overloading and aggregated toward the lower part of the jar. Under the influence of the magnetic field, a culture of this sort showed the streaming movements distinctly. There was this difference, that an aggregation was formed overhead of the field of the magnet at the water surface. The animals which are oriented upward continue in many cases to the top and there may remain, often forming a dense ring at the water's edge. These are therefore an aggregation of active animals able to maintain themselves at the top, and contrasting with the aggregation in the lower outside corner, consisting of sluggish individuals. The latter sort, if near enough to the field of the magnet are sometimes noticed to move as if passively pulled by its attraction.

3. *Ingestion of iron for a brief period, 20-30 seconds.*

In this length of time only a light load is taken in. With the cultures used this produced a marked upward tendency in the control, so as to leave the lower region approximately free from *Paramoecia*. When this culture was brought under the influence of the magnet it appeared that the upward streaming was for a short time visibly greater on the side of the magnet, but there was no noticeable compensating movement downward, and in consequence the upward streaming was of short duration. The aggregation above the magnetic pole was distinctly greater than elsewhere, so that this case gives only a single region of aggregation.

THEORIES OF GEOTROPISM OF PARAMOECIUM —

Various explanations have been offered for the geotropic response, such as sensitiveness to the difference in pressure between the upper and lower portions of the organism; sensitiveness to the greater resistance encountered in swimming upward than downward; response to internal localized stimuli by heavier particles in the endoplasm—the statocyst theory. All have taken for granted that orientation to gravity was brought about by a response to some sort of stimulus.

Verworn is credited by Lyon with having earlier held that the geotropic response of *Paramoecium* was explicable on the basis of the form and structure of the organism, a view which he is said to have later abandoned. The original reference is not at hand.

These theories are discussed by Davenport, with the exception of the later one of Lyon, and he credits the mechanical factor as having some influence at least in producing the geotropic orientation.

DISCUSSION OF RESULTS

In presenting what appeared to the writer to be valid reasons for accepting the view that in the case of experiments with loaded animals the geotropic tendency is a result of passive orientation rather than a response to any form of stimulus by gravity, I would not have it supposed that I am opposing the possibility of the action of gravity as a stimulus under any conditions. Inasmuch as evidence has been offered in this paper for the action of gravity as a stimulus upon heavily loaded animals tending to check their upward movement, it would be unwise to harbor a predilection against the possibility of its acting as a stimulus to account for movement in either direction.

Jennings instances the case of the geotropic collection of *Paramoecia* in distilled water which give the avoiding reaction on starting to move downward and so are oriented upward again. This furnishes an opportunity to compare my results with those of Jennings. In no case have I a record of a complete geotropic collection at the top of the tube in my experiments with iron filings and ordinary water. There have been aggregations toward the top with no sharp dividing line and the animals all show active swimming movements in all directions, except those which collect on the walls of the vessel and in the surface film. Hence there is no possibility of recognizing the geotropic response *per se* as there is in the pure form of the reaction described by Jennings. There is however abundant opportunity to observe the gradual swinging from a horizontal to a vertical path among such animals and the recognition of it as a prevailing type of movement. I have given the chief reason for using ordinary water in these experiments instead of distilled in which the pure response may be elicited. It is, to repeat, because the greater negative tendency of the properly loaded

Paramoecia is measured by comparing their behavior with an ordinary control. Control experiments in ordinary water may make quite complete surface aggregations after a considerable time, but usually the reaction is gradual, while the treated cultures move up often with surprising quickness. I have had cases of nearly complete surface collections of treated animals with only a few scattering individuals not included, but when these occurred after a half hour or more I was inclined to suspect the denseness of the aggregation was due to the formation of an acid area about them. Distilled water also has its disadvantages in causing their ultimate death and some amount of contraction of the body and sluggishness of movements. According to Jennings the avoiding reaction given when starting to move downward is the geotropic response *per se*. It would tend to produce an effect of "orientation by exclusion" to use his terminology. It appears to the writer that the mode of passive orientation would only supplement the geotropic response and not exclude it. The animal might swing passively into the oriented position during its ordinary movements and since this would be a position of stable equilibrium, it might happen under certain conditions,—say in pure water, that movement out of the position of stability might be able to induce a stimulus. Orientation by exclusion is not permanent. But a position of stability in the water does give permanence to the orientation and accounts for the quite regular movements in parallel lines, which is best shown under the magnetic control by heavily loaded animals in the upward stream.

Jennings also points out that resting animals on the bottom or in contact with the sides of a vessel or in the surface film all show characteristically the oriented position. This may surely be taken as corroborative evidence for the acceptance of the view that there is a position of equilibrium to gravity which is passively assumed. This fact accords well also with the other observation that the oriented position is assumed by animals moving quietly in narrow spirals and that any disturbance of their movements by stimulation annuls the passive orienting tendency. It must be remembered that the normal reaction is a very delicate one. As Jennings says: "Whatever the cause for the reaction to gravity, the stimulation it induces is evi-

dently very slight and its effect is easily annulled by the action of other agents."

SUMMARY OF RESULTS

1. Paramoecia which have ingested a certain amount of finely divided iron show temporarily an increased upward orienting tendency which persists as long as the particles remain in the posterior end, and tends to disappear as they become scattered more evenly through the endoplasm.

2. The passive sinking of the posterior end is able to orientate the animal into a position of gravity equilibrium with anterior end up, only when it is moving in a narrow spiral or nearly straight path. Overloaded individuals which are impeded in their upward movements by the load begin to move in a broad spiral and so change their course eventually to a downward direction in the path of least resistance.

3. A magnet placed at one side of a jar containing Paramoecia which have ingested iron causes an upward streaming in the stronger part of the field. Those heavily loaded animals which move upward in this stream after dispersing above into the weaker part of the magnetic field tend to sink again and cause a return circulation to the bottom.

4. The magnet is effective in producing this circulation by diminishing the effect of gravity on animals containing iron. It also exerts a passive pull upon them and they gradually swing into their finally oriented position in a vertical path under the combined influence of the magnet and gravity. The oriented path is consequently a curve.

REFERENCES

- DAVENPORT, C. B. Experimental Morphology, vol. 1, N. Y.
HARPER, E. H. The Geotropism of Paramoecium. *Jour. of Morph.*, vol. 22, 1911. no. 4, pp. 993-1000.
JENNINGS, H. S. Behavior of the Lower Organisms. New York. 1906.
JENSEN, P. Ueber den Geotropismus Niederer Organismen. *Arch. f. d. ges. Physiol.*, LIII, 428-80.
LYON, E. P. On the Theory of Geotropism in Paramoecium. *Amer. Jour. Physiol.*, 1904. XIV., 421-32.
MOORE, A. Some Facts Concerning the Geotropic Gatherings of Paramoecium. 1903. *Amer. Jour. Physiol.*, IX, 238-244.

FOOD AND CHEMICAL REACTIONS OF THE SPOTTED NEWT, *DIEMYCTYLUS VIRIDESCENS*

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Although Gage (3), Jordan (4), Monks (5), Pike (7), and others have published observations upon the habits of this common newt the writer is not aware of any experimental observations upon the feeding habits nor upon the chemical reactions in general of *Diemyctylus*.

The species is fairly common in the neighborhood of Morgantown, and about a dozen specimens, all in the green stage, were collected late in the autumn and kept in an aquarium in the laboratory, where the experiments described below were carried on. They were fed at intervals with earthworms and bits of raw meat, and seemed to remain in a perfectly healthy condition.

Merely as a matter of convenience the following descriptions will be given as a series of experiments.

Experiment I. The object of this experiment was to determine whether the animals found their food by sight or by smell, using the latter term to designate what Miss Washburn calls the "telaesthetic sense" of aquatic animals.

Most of the tests were made upon three animals that were selected because of their especially healthy appetites, although they had not been subjected to any especial starving process, but had been fed, or at least offered food, at the same intervals as the rest.

The first animal followed actively a small roll of filter paper held in fine-pointed forceps and seized it once or twice, but let go of it immediately. It reacted the same way towards similar rolls of white and of black raw cotton, but by this time seemed fatigued so that it scarcely noticed a roll of yellow cloth. A piece of raw meat of similar size and shape was now offered; it was immediately seized before it could be withdrawn and was held to so tightly that the animal was lifted entirely out of the water before it let go its hold.

A day or so later, after snapping again and again at a piece

of meat, it half swallowed a piece of filter paper, but immediately disgorged it. It then seized and swallowed a piece of meat.

Two days later it followed and seized but immediately dropped a piece of yellow cloth; it then paid no attention to a roll of black cloth, but snapped a piece of meat when offered it.

The second animal was tested with the same small pieces of paper, cloth, etc. When offered the roll of filter paper, it followed it about in the aquarium quite actively, finally seizing and half swallowing it, but immediately disgorging. It then seized and completely swallowed a piece of white raw cotton, after which it refused to follow either black or yellow cloth, and only followed the meat after some coaxing.

Two days later it followed a piece of meat and snapped at it so suddenly that it was seized and swallowed before it could be withdrawn. It then seized and half swallowed a piece of filter paper, but disgorged it. A piece of filter paper soaked in meat juice that was now offered, was seized and swallowed; this filter paper was disgorged and was found in the aquarium two days later, at which time the animal followed and snapped at a roll of yellow cloth, but after once seizing it, refused to follow it again; a piece of meat that was now offered was followed and snapped at again and again, but was withdrawn each time before the animal could get it. A piece of black cotton which was offered was seized, but immediately disgorged. It now refused to follow a piece of white paraffin, but tried to seize a piece of meat when it was offered. The paraffin was seized by another animal, but was immediately dropped.

A third animal was tested in the same way as has just been described for the first two and acted in essentially the same way. It would follow small tasteless objects of various colors and would often seize them, but usually disgorged them almost immediately. Usually after snapping at the tasteless objects a few times the animals refused to follow them longer, but in such cases they would nearly always follow and try to seize a piece of raw meat of the same size. The color of the tasteless objects seemed to make little or no difference in the reaction.

Generally after swallowing one good-sized piece, whether of meat or of one of the indigestible objects, the animal could not be induced to touch anything more at that time.

The same three animals, and several others, were tried with a small piece of apple. Several of them followed the apple and one or two snapped at and half swallowed it, but it was always disgorged before it was completely swallowed. Several animals that paid no attention to the apple immediately followed and snapped at a piece of meat.

A small piece of caramel that looked almost exactly like the meat was followed and snapped at by some of the animals, but none of them would swallow it. Many of the animals that paid no attention to the caramel seized and swallowed, immediately after, a piece of meat.

The entire lot of animals was tried with pieces of meat and pieces of earthworm of the same size. Most of the animals seized, or tried to seize, the meat and earthworm, offered alternately, and no difference in reaction towards the two could be noticed. As in nearly every experiment, there were a few animals that refused to eat, and those that refused the one refused the other, in this case. None of the animals seemed to show any preference for the earthworm, a natural food, over the raw beef, food to which they were, of course, not accustomed in their natural haunts.

Several small pieces of meat and of earthworm were wrapped in filter paper and thrown into the aquarium with a number of animals. These small bundles, all looking alike, remained untouched for several days, when they were removed because they had begun to foul the water.

Experiment 2. As a further test to see whether the animals were guided by a sense of smell or taste, two kinds of beef extract were made; one by boiling meat in water and filtering the resulting broth, the other by grinding pieces of raw meat in a mortar with a little water and filtering the bloody liquid that was thus obtained. As the animals reacted the same to the two liquids, the latter was used in nearly all of the experiments. The method of using the meat fluid was to squirt a little of it from a fine-mouthed pipette upon the tip of the head of an animal that was lying still in the aquarium. As in Experiment 1, most of the trials were made upon three or four animals that responded more quickly than the rest, but all of the animals acted in essentially the same way.

When a little of the fluid was ejected upon the head of an animal

it often responded by snapping its jaws, even after the pipette was withdrawn. If the pipette were held still, very close to the nose of the animal, it would often be seized by the animal and held in the mouth, just as were the tasteless substances in Experiment 1; this seldom happened when a clean pipette was held close to the nose of the same animal. No attention was paid to a jet of pure water squirted against the nose, nor to a jet of water in which cane sugar had been dissolved.

In many cases the fluid in the water, after the withdrawal of the pipette, caused the animal to put its nose to the bottom, in its characteristic way, as though searching for food; and with one animal the fluid not only caused this reaction, but it caused the animal to rub over the bottom with open mouth, and to snap, again and again, at spots in the glass bottom.

In some cases the pipette was held in such a position that it could probably not be seen by the animal, but the juice produced the same reaction as before.

In a few cases an animal which failed to respond to the meat fluid responded very quickly to a piece of meat, which would seem to indicate that sight is perhaps as important as smell and taste in securing food; later experiments, described below, seemed to disprove this, however.

Raw meat juice that had been allowed to stand until it had become rancid enough to have a decided odor, caused a negative response in nearly all of the animals. With these same animals that had withdrawn from the stale juice, the fresh juice caused in nearly every case a positive response such as has been described above—in one or two animals an extremely active snapping motion. The stale juice had no effect except upon the head of the animals.

An extract was made by grinding earthworms in a mortar with a little water and filtering the resulting fluid. This liquid was used in a pipette just as was the meat extract, first the meat and then the earthworm extract, but no difference in the reactions of the animals could be detected to show that they preferred one rather than the other.

In securing food, then, it is probable that *Diemyctylus* uses both sight and the telaesthetic sense, perhaps the latter more than the former. After the food has been located and seized, a chemical sense, taste or smell, usually decides whether it shall

be entirely swallowed or not, though as has been seen above, the animal frequently swallows substances that would seem to have no taste or smell whatever. They sometimes seem to perceive by sight, objects, meat, etc., that are several centimeters distant; but the telaesthetic sense apparently operates only at much shorter distances.

REACTIONS TO LIQUID CHEMICALS

In the following experiments the reactions of the animals to all of the chemicals used, representing the various tastes as we know them, sweet, sour, bitter, etc., were tried in the same way; the solutions, in varying strengths, were squirted from a small pipette upon different parts of the animal as it lay quiet in the bottom of the aquarium in about five centimeters of water. As the animals are naturally quite active, especially in strong light, it was necessary to work in a rather dim light. Owing to this same activity, the animals usually became so restless after a few stimulations, that it was not possible to make a large number of tests at any one time; this made experimentation rather slow.

Since the animals are only about nine centimeters in total length, it was not possible to stimulate them in as many different places as was done by Sheldon (8) with the dogfish.

As a matter of fact, experiments failed to show, with the exception of the anterior part of the head, any greater sensitiveness in one part of the body over another. It was at first thought that the region of the base of the tail was more sensitive than any part except the head, perhaps because it was impossible, because of the small size of the animal, to stimulate that region without stimulating the region of the cloaca; but further experimentation failed to verify this early supposition.

The reaction to all of the chemicals used, with the exception of those described above under the head of food reactions, were negative. In the case of sugar only was there no reaction, and, in fact, even there a sort of negative reaction was seen, as will be described later.

The reaction when a chemical of sufficient strength was squirted upon the tip of the head, varied from a slow withdrawal backwards, when a very dilute solution was used, to a sudden withdrawal accompanied with a violent shaking of

the head from side to side, when a strong solution was employed. If the stimulus were of unusual strength, the animal might roll over and over, as though in great agony, and then dart away to a distant part of the aquarium. Chemicals of this strength were seldom used more than once, because of the possible injurious effect upon the animal.

A weak stimulus on the hinder parts of the animal usually caused a slow motion forward to escape the stimulus, though occasionally a slight twitching was the only response; the twitching was usually followed, however, by the forward motion if the stimulus were continued. A more violent stimulus of this region caused a sudden start forward, and the animal very frequently reached back and bit at the spot stimulated. A still more violent stimulation produced not only the biting reaction, but caused the animal to roll over in apparent agony as was noted above in connection with the stimulation of the head.

A remarkable amount of variation was noted in the different animals in regard to their sensitiveness to chemical stimulation, both on the head and on the body regions. A stimulus that would cause one animal to respond in a violent way, as though it caused considerable pain, would have almost no effect upon another animal. The same animal at different times also showed considerable variation in sensitiveness, owing, it may be supposed, to variations in the physiological condition. It is possible that the variation in sensitiveness may be due partially to variations in the cuticle, though this could not be definitely determined. At any rate, the cuticle is shed with remarkable frequency, and it may be that when it is beginning to loosen preparatory to being cast, it may make the animal less sensitive to stimulation.

Experiment 3. To test the reaction of the animals to what is to us a sweet taste a 10% solution of cane sugar in distilled water was used. This concentration makes a very sweet solution, in fact almost a syrup, but no reaction proper was obtained by prolonged stimulation of either head or body regions, though all of the animals on hand were tried. That the solution was, however, not entirely without effect seems possible from the fact that while the animals in this experiment frequently snapped at and even seized the empty pipette or one containing pure water, they never acted in this way towards a pipette containing the sugar solution. It would seem that the sugar repelled

them enough to keep them from snapping at the pipette, but not enough to cause them to withdraw from the jet of sugar solution when squirted against them.

Experiment 4. This experiment was to test the reaction of *Diemyctylus* to a bitter solution, and a nearly saturated aqueous solution of quinine sulphate was used. No reaction at all was obtained except when the solution was squirted upon the head. In this case there was sometimes a rather slow withdrawal, but usually the reaction was quite marked, the animal shaking its head in evident discomfort, or with what in the case of man would probably be disgust.

After reacting negatively to the quinine the animal would usually respond in the ordinary way to meat juice that was offered in the same manner. One animal that paid no attention to meat juice reacted, though not actively, to the quinine solution.

Picric acid was not tried because, as has been shown by Sheldon, the acidity is apt to cause a more marked reaction than the bitterness.

Experiment 5. As an example of a neutral saline solution sodium chloride was used. Nine animals were used, and a 4% solution of the salt in distilled water was first employed. This solution when squirted upon the head caused a negative reaction in all of the animals. In two or three the reaction was quick and violent, the animal shaking its head in evident discomfort. In others the reaction was quick but not violent; and in others the reaction was slow, taking place only after an entire pipette or more of the solution had been used.

On other parts of the body the 4% solution caused in all but one or possibly two, animals a long-delayed but usually marked negative response. In some animals the response consisted in simply a twitching of the part stimulated, in others there was a slow withdrawal from pipette, while in others the animals bit at the point stimulated; but even in the animals where the latter response took place, it was usually so slow that one or more entire pipettes of the solution had to be used before the reaction occurred.

A 2% solution caused definite responses in all but three of the animals when used upon the head, though the reaction was not

so marked as with the 4% solution. No certain reaction was obtained with this solution upon other parts of the body.

A 1% solution gave a fairly quick though not violent response in the case of a single animal, used, of course, upon the head. Two other animals slowly withdrew from the stimulation after long delay. The remaining animals gave no response at all to this solution, which is probably about the limit of dilution for this salt.

Judging from the comparative reactions of the hydroxides of potassium and sodium it seemed likely that the animals would have reacted to the potassium chloride in the same way as to the sodium salt, so the former was not used.

It is of course evident that in all of these experiments the solutions are more dilute than is indicated by the time they actually come in contact with the animal, since they must be somewhat diluted by the surrounding water, even though the pipette be held as close to the animal as possible.

Experiment 6. To test the animals for alkalies solutions of sodium and potassium hydroxides in distilled water were used. The reactions obtained in the two cases were of the same character and, apparently, of the same intensity. The first experiments seemed to show a slightly greater sensitiveness to the potassium solutions, but later experiments showed that this was not the case. Since, therefore, the reactions were the same in the two cases, only the experiments with the potassium hydroxide will be described. Nine animals were used in this experiment.

A 2% solution of the potassium hydroxide when squirted on the head of an animal caused instant and extremely violent reaction, as though the animal were in great pain. A very small quantity of the solution was sufficient to cause this reaction, and in no other solution of the same strength was the reaction so violent. When this same solution was brought in contact with the body or tail of the animals the reaction was almost as quick and quite as violent as on the head, the animal writhing and biting at the spot stimulated as though in agony.

A 1% solution gave reactions upon head and body that were nearly as marked as those for the 2% solution, and a .5% solution gave nearly the same reactions for head and body, except that they were slower in starting.

All nine of the animals responded to a .25% solution, but more slowly and less violently than in the preceding cases. All nine animals responded fairly quickly and violently to a .125% solution when the head was stimulated; all but one responded when the tail was stimulated, and two of these bit at the spot affected.

All nine animals responded fairly strongly to head stimulation with a .0625% solution, though some responses were very slow. Three or four gave no response to tail stimulation, though one which did respond bit at the spot stimulated.

All of the animals responded to a .03125% solution on the head, though the response was very slow and usually not strong. Only one animal responded to stimulation of the tail, but that one bit at the spot stimulated as though the irritation were considerable.

All but two of the animals responded to a .015625% solution when the head was stimulated; the reaction was, of course, very slow. No reaction was obtained from any of the animals when the fluid was squirted against the tail.

A .0078125% solution produced a response in only one animal when the head was stimulated, and no response was obtained from any of the animals when other parts were stimulated.

Experiment 7. For reactions to acids various strengths of hydrochloric and glacial acetic were tried. Since no difference in the reactions was noted, except that, as might be expected the hydrochloric acid acted more strongly for a given concentration, the experiments with only the acetic acid will be described.

As was said above, experiments were tried to determine whether one part of the animal was more sensitive to chemical stimulation than another, but with the exception of the head, all parts of the body seemed to be about equally sensitive. Whether it were the nostrils, mouth, or eyes that caused the greater sensitiveness of the head it was difficult to determine, since, on account of the small size of the animals, it was almost impossible to stimulate one of these structures without the other. By carefully controlling the direction of the jet from the pipette it was possible to cause most, if not all, of the fluid to escape the eyes, and no difference was noticed in the reactions of the animals so stimulated from those in which the jet was directed upon the top of the head as a whole. The relative sensitiveness of the

nostrils and mouth will be discussed later. By directing the jet caudad the eyes could be stimulated with probably but little stimulation of the nostrils and mouth; no certain difference in reaction could be determined from what was seen when the jet was directed in the other direction as noted above.

A 10% solution of glacial acetic acid was first used, and this was gradually diluted until no reaction was obtained; this dilution was made in all cases with distilled water. Twelve animals were used, the experiments extending over several days. The water was changed after each set of experiments.

The 10% solution, as might be expected, caused violent and almost instantaneous reaction when squirted upon the head, while upon the body it caused active though much less violent responses.

A 3% solution caused fairly quick reaction upon the body, and much more violent reaction upon the head, often a violent shaking of the head taking place. This dilution of the acid is distinctly sour but not irritating to the human tongue.

A 1% solution on the head caused a quick though less violent reaction than in the preceding. Upon the body it caused slow reactions, and in none of the dilutions lower than this one was there any certain response. It will be noticed how much more sensitive the animals are to weak solutions of alkalis than to weak acids. The 1% acetic acid has a faintly sour taste.

A .3% caused a moderately quick response upon the head, but, as was said above, no certain response upon the other parts of the animal. A finger moistened with this dilution of acid and touched to the human cornea caused a brief but decided stinging sensation.

A .075% solution caused in every animal a moderately prompt and decided response when squirted upon the head. When squirted upon the human tongue it causes a barely discernible sour taste, and in the human eye causes scarcely more sensation than would a drop of cold distilled water.

A .0375% solution caused a fairly quick and decided response in all animals, in a few cases with a shaking of the head in the manner characteristic of a disagreeable sensation.

A .01875% solution produced in all animals a negative response, generally fairly quick, and sometimes quite violent. This solu-

tion still has a faintly sour taste to the human tongue in quantity, but in the human eye produces no more sensation than cold water.

A .009375% solution produced in all animals a responses though not a very decided one. Squirted upon the human tongue this solution produces no sensation of acidity, though in larger quantities a faintly sour taste may still be discerned.

A .0046875 solution produced reactions in all animals, though in most cases so slow that several pipettes full had to be squirted upon the head before the animal withdrew.

A .00234375% solution, containing about one part of the pure acid to 42000 parts of distilled water, caused very slow responses, and is probably about the limit of dilution that will cause response, in these animals, though it is possible that under the proper conditions they might be still more sensitive. It is only by alternately drinking distilled water and the diluted acetic acid that a sour taste can be discovered in such a great dilution. Without the pure water for comparison the taste could not be detected, and it would not be noticed even in this case unless it were being tasted for.

Experiment 8. As a chemical that would not naturally be classed as sweet, sour, or bitter, but which produced a stinging sensation, alcohol was used.

10% ethyl alcohol, which produces a decided stinging sensation in the human mouth, caused a reaction with all the animals tested (nine) both upon the head and upon the tail. The head reactions were rather slow, and not as violent as might have been expected, when the violence of the reactions to weak acids and alkalies is remembered. The reactions from tail stimulation were usually even slower, as would be expected, though they were sometimes characterized by the biting motion mentioned above.

Only one of the nine animals reacted to 5% alcohol when the tail was stimulated. Only one of the nine failed to react to that grade of alcohol upon the head. Two of the latter reacted fairly promptly, the rest very slowly, only after one or more entire pipettes of alcohol had been squirted against the head.

None of the animals reacted to 2% alcohol when it was used upon the tail, and only four of them reacted when the head was

stimulated. Of these four three reacted in a very slow uncertain way, while the fourth responded fairly promptly.

The only animal that responded at all to 1% alcohol was the one just mentioned as responding fairly quickly to the 2% grade; 1% is, therefore, probably the minimum percentage of ethyl alcohol that will cause reaction in these animals.

Experiment 9. The effect of cocaine was tried both to see what the effect might be, and to try to distinguish between the sense of taste and that of smell.

Thinking that the soft moist skin of *Diemyctylus* would be at least as sensitive to cocaine as the harsh skin of the dogfish that Sheldon used, a 2% solution was first tried. This concentration was found by Sheldon to produce insensibility first to touch and later to chemical stimulation. The cocaine was first tried by painting it over the nasal region of animals that had been taken from the water and allowed to dry for a few moments. In this process it was almost certain that the cocaine must have entered the nasal chamber through the nostrils. After a few minutes the animals were replaced in the water and were tested with a 1% solution of acetic acid, such as has been mentioned in preceding experiments, every ten minutes or more during several hours. The cocaine had no apparent effect whatever.

Thinking that possibly the sensitiveness of the head, after the nasal region had been treated with cocaine, might be due to stimulation of the eyes or the lips by the acetic acid, in spite of the care that was exercised to direct the stream from the pipette in such a direction that it should stimulate only the region that had been painted with the cocaine, the experiment was tried of painting the entire head, dorsal and ventral, including the eyes, with the 2% cocaine. The result was the same as before.

In other animals the cocaine of the same strength was used upon the tail; about half an inch of the tail, just caudad to the posterior appendages, was painted entirely round the animal and including the cloaca. This region was tested with the 1% acetic acid every fifteen minutes for several hours, but no change in its sensitiveness could be detected.

Another series of experiments in which a 5% solution of cocaine was used in the same way that the 1% had been used gave no difference in reaction to the 1% acetic acid. A 10% solu-

tion was then used in the same way, with the same negative result. It was then concluded that the skin of this salamander is, like the human skin, and unlike that of the dogfish, not susceptible to cocaine when applied superficially as may be done with a mucous membrane.

Experiment 10. In hopes of being able to distinguish between the sense of smell and that of taste a 5% solution of cocaine was used in the manner about to be described. Owing, however, to the fact that the posterior nares, as in the frog, are comparatively wide and are situated far forward in the roof of the mouth, it is probable that in this experiment the cocaine that was used in the mouth always affected the nasal chamber about as much as it did the oral mucous membrane; and that, as was said above, when the cocaine was applied to the anterior nares it leaked down into the mouth.

Since the anterior nares are very minute, scarcely large enough to admit an ordinary pin, it was useless to try to stop them up with cotton as did Sheldon (9) in his experiments upon the sense of smell in the dogfish.

The results obtained in this experiment were, as will be seen, somewhat conflicting, but they will be described as briefly as possible. An animal that snapped vigorously at a bit of meat was removed from the water and a small wad of raw cotton saturated with 5% cocaine, was put into its mouth and held there for about two minutes. The animal was then returned to the water and offered the bit of meat; it paid no attention whatever to the meat, though it was presented to its nostrils at intervals of from ten to sixty minutes during the next seven hours. It also responded very slowly and weakly to 1% acetic acid during the first half hour after the removal of the cotton from the mouth.

Another animal that also snapped quickly at a bit of meat, thus showing that it was hungry, was removed from the water and a wad of clean raw cotton, wet with pure water, was put into its mouth as was done with the cotton wet with cocaine in the first animal. On being replaced in the water this animal immediately snapped at the meat, and did so again at the end of ten minutes; this seemed to indicate that the raw cotton had no effect upon the feeding habits of the animal. The cotton was now soaked in 5% cocaine and again introduced into the

animals' mouth where, as in the case of the clean cotton, it was held for two minutes. When the animal was returned to the water it paid no attention to the meat, nor to a 1% acetic acid solution. After five minutes it still paid no attention to the meat, but gave a weak response to 1% acetic acid. Half an hour later it was still indifferent to the meat but gave a fairly strong response to the acid. Two and a quarter hours after this it still refused the meat, but an hour later it again snapped at the meat, and continued to do so at intervals of an hour for the rest of the day, as though it had entirely recovered from the effects of the cocaine. The next day both of these animals refused to eat.

The third animal acted in about the same way as the two that have been described, except that on the second day it seemed to recover from the effects of the cocaine in a much shorter time than did the first two animals. After the first application of cocaine it failed to respond to meat for about three hours.

The fourth animal on the first day reacted as did the three preceding, but on the second day after removal of the clean cotton the animal refused to eat though tried at intervals for more than two hours. Whether the cotton had anything to do with this reaction cannot be said with certainty. Two days later this animal, after snapping at a piece of meat, was removed from the water and its nostrils were painted for three minutes with a 5% solution of cocaine, a camel's hair brush being used. On being returned to the water it refused meat for more than half an hour.

The fifth animal after removal of the clean cotton from its mouth refused meat for only a few minutes then snapped at it. It was then removed from the water and its nostrils painted, as in the preceding animal, with cocaine; it then refused meat for the rest of the afternoon, though offered it at intervals for more than two hours. Two days later this animal after being treated with cocaine in the same way snapped at the meat in less than half an hour after being returned to the water.

The sixth animal on three occasions, after snapping at the meat, was treated with the cocaine as in the preceding animal, i. e., had its nostrils painted with the 5% solution. On two of these occasions the animal snapped at the meat in half an hour

or less; on the other occasion the animal refused food for the rest of the afternoon, about three hours.

The seventh animal on one occasion snapped at the meat immediately after being returned to the water; at another time it snapped at the meat within an hour of the time of application of the cocaine to its nostrils.

The eighth animal snapped at the meat a little more than half an hour after applying the cocaine to its nostrils.

Two other animals that were tried in the same way snapped at the meat within half an hour after being returned to the water.

Four animals in which a wad of raw cotton saturated with 5% cocaine was held in the mouth for three full minutes, were all thrown into such a state of coma that they were thought to be dead; one of these recovered in about an hour; the others required two hours to regain their usual activity.

Of two other animals in which the cotton with the 5% cocaine was kept in the mouth for one-half minute, one refused meat for the rest of the afternoon, about an hour, while the other snapped at the meat in less than half an hour.

While these experiments are not altogether satisfactory, it will be noticed that the cocaine introduced into the mouth inhibited in every case except one, the feeding reaction for an hour or more, and the shorter time in the exceptional case may have been due to the fact that the cotton was not kept in the animal's mouth long enough.

Whether the inhibition was due to the effect of the cocaine upon the nerves, or whether it was merely due to the general effect upon the animal as a whole, it is difficult to say, but the serious state into which several of the animals were thrown by too prolonged action of the cocaine, as described above, would seem to point to some general disturbance of the system that might incidentally inhibit the feeding reaction.

The application of the cocaine to the nostrils caused, as might be expected, a much more temporary inhibition of the feeding response, the failure to react to meat seldom lasting for more than half an hour, and in many cases the reaction was delayed an even shorter time. Just how much of the cocaine solution would penetrate the nasal chamber through the tiny external nares, it is impossible to determine, possibly very little.

Judging from the relative lengths of the inhibited periods,

it would seem that either the animal scents its food more through the mouth than the nostrils, or that more of the cocaine found entrance into the nasal chamber from the cotton held in the mouth than entered through the nostrils when they were painted with the solution. Later experiments indicate that the latter is the case. This is assuming that in both cases the inhibition was nervous rather than a general disturbance of the system. The next experiment supports the view that the inhibition is due to the effect of cocaine upon the nerves rather than a general depression of the system.

Experiment 11. In this experiment five animals were used, and all were treated in exactly the same way. They were removed from the water and a wad of raw cotton wet with 5% cocaine was held in the mouth for half a minute, then the nostrils were painted with the same solution of cocaine for one to two minutes. When returned to the water all of the animals were more or less sluggish, four of them only slightly so, while the fifth was decidedly sluggish. After the cocaine treatment, the animals were subjected to a jet of acetic acid of a strength that in normal animals would cause quick and generally violent reaction, the jet being, of course, directed upon the anterior region of the head. Since four of the five animals reacted in practically the same manner, animal number 4 will be described as a type.

At 8.25 A. M., about five minutes after being returned to the water, the animal failed to respond to an entire pipette full of .25% acetic acid that was slowly squirted against its head. At 8.55 A. M. it responded very slowly to .5% acetic acid similarly used. At 9.10 A. M. it responded fairly quickly to .5% acid, but still much more slowly than normal. At 9.45 and 10.45 A. M. the response was still about the same as at 9.10 A. M. At 5.00 P. M. of the same day the response to the .5% acetic acid was as quick as in the normal animal, and the same was true at 10.30 A. M. the next day.

It may be possible, then, that the cocaine used in this way inhibited the chemical sense in the nasal and oral mucous membranes for a couple of hours, and during this time the slow and feeble reactions were merely those due to the stimulation of the skin over the head, which was little more sensitive than that of the rest of the body.

Experiment 12. To further test the importance of smell, using that term in the usual sense, in securing food, four animals were selected. It was found by dissecting preserved specimens that, by inserting the points of a fine pair of scissors into the two posterior nares, and cutting the intervening tissues, both olfactory nerves could be sectioned with one quick cut. With the four selected animals this was done, after administering just enough ether to keep them from struggling.

In three of the animals there was apparently no bleeding, but in the fourth the scissors failed to work properly, and there was considerable loss of blood. This animal was somewhat slower in recovering its activity and was found dead in the aquarium at the end of the second day. So far as observed, however, its reaction to food and acid were about the same as in the other three. These three recovered from the ether in a few minutes and the morning after the operation they were as active as ever, and gave no indication of being any the worse for the operation. Once or twice a day for more than a week they were tested with a bit of raw meat, but in no case attempted to seize it. Two of the animals paid no attention whatever to the meat, while the third, on two or three occasions, followed the meat (and also a piece of filter paper) without snapping at it. Juice from raw meat and from earthworms, described above caused no reaction whatever, though samples of both caused the snapping response in normal animals.

After having been without food for about two weeks the animals, stimulated by extreme hunger, began to snap at meat or filter paper that was moved near them. If permitted to do so they would swallow the filter paper as readily as the meat. They would not seize either meat or paper unless it was in motion.

While it is hard to understand why, if sight be the sense used, cutting the olfactory nerves should make an animal less apt to follow a bit of meat or a tasteless piece of paper, the absolute refusal of these animals to eat, after severance of the olfactory nerves, seems to show that the olfactory sense is the one mainly used by *Diemyctylus* in recognizing food.

For two or three days after the operation, the response to a .5% solution of acetic acid on the head was slower than in the normal animals; but after that time the negative reaction was apparently as quick and as decided as in animals with uncut

olfactory nerves. This would seem to indicate that the greater sensitiveness of the head region over other parts of the body to chemical stimulus, while it may be due merely to a greater sensitiveness of the skin of that region, is probably due to the sensitiveness of the nasal and oral mucous membranes, and not to any olfactory sense proper.

SUMMARY

1. *Diemyctylus* uses both sight and an olfactory sense in securing food, though the latter is apparently the more important.

2. The normal animal will follow and sometimes seize small bits of cotton or cloth of various colors, but will seldom swallow them; and when such objects are swallowed they are later disgorged. When fatigued with these objects so that it will no longer snap at them the animal will almost always seize and swallow bits of raw meat or earthworm.

3. There seems to be no difference in reaction between bits of raw meat and earthworms.

4. There is about the same response to filtered meat juice (both raw and cooked) as to the filtered juice from crushed earthworms. The response consists in snapping at and seizing the end of the pipette from which the juice is coming; also in snapping and searching motions after withdrawal of the pipette.

5. With the exception of the head all parts of the body seem to be equally sensitive to chemical stimulation. The head is much more sensitive than the rest of the body, even after the olfactory nerves are cut.

6. There is no definite reaction to a strong solution of sugar.

7. To a saturated solution of quinine a fairly strong negative reaction is obtained when the head is stimulated, but no reaction is obtained from other regions.

8. Negative reactions to a 1% sodium chloride solution are obtained from some animals when used upon the head. No reactions are obtained from stimulation of other regions with a solution more dilute than 4%.

9. 2% potassium hydroxide solutions cause quick and extremely violent reactions upon both head and body. The most dilute solution that causes reaction when ejected against the head is .0078125%. The reactions to this reagent are more violent than to any other chemical tried of equal percentage.

10. Negative reactions to acids are also very marked, and take

place with high dilutions. One part of acetic acid in about forty-two thousand parts of distilled water give weak reaction upon the head.

11. 1% ethyl alcohol is the weakest grade that causes negative reactions. The reactions to higher grades are slower than would be expected from the stinging sensation produced by these grades upon the human mucous membranes.

12. Cocaine, even up to 10%, has no apparent effect upon the skin of *Diemyctylus*. A 5% solution of cocaine applied to the nasal and oral mucous membranes temporarily inhibits the feeding reaction, and diminishes the sensitiveness to acid solutions squirted upon the head. This result may be due to the general effect of the cocaine upon the system rather than upon the nerve endings of the nose and mouth.

13. Animals in which both olfactory nerves are cut refuse, for two weeks, to eat meat or earthworms, or to pay any attention to the juices from these; but after recovering from the operation the response to .5% acetic acid is apparently unchanged.

BIBLIOGRAPHY

1. BAWDEN, H. H. Bibliography of the Literature on the Organ and Sense of Smell. Jour. Comp. Neur., Vol. XI, pp. II-XL.
1901.
2. BELL, J. C. Reactions of Crayfish to Chemical Stimulation. Jour. Comp. Neur. & Psychol., Vol. XVI, pp. 299-326.
1906.
3. GAGE, S. H. Life-History of the Vermillion-Spotted Newt. Amer. Nat., 1891. Dec., pp. 1084 & fol.
4. JORDAN, E. O. The Habits and Development of the Newt (*Diemyctylus viridescens*). Jour. Morph., Vol. VIII, pp. 269-366.
5. MONKS, SARAH P. The Spotted Salamander. Amer. Nat., Vol. XIV, pp. 301-374.
1880.
6. PIKE, COL. NICHOLAS. Some Notes on the Life-History of the Common Newt (*Diemyctylus miniatus viridescens*). Amer. Nat., Vol. XX, pp. 17-25.
1886.
7. REESE, A. M. The Habits of the Giant Salamander. Pop. Sc. Month., April, 1903. pp. 526-531.
8. SHELDON, R. E. The Reactions of Dogfish to Chemical Stimuli. Jour. Comp. Neur. & Psychol., pp. 273-311.
1909.
9. IBID. The Sense of Smell in Selachians. Jour. Expr. Zool., Vol. X, No. 1, 1911. Jan, pp. 51, 62.

DISCUSSION OF CERTAIN QUESTIONS RAISED BY
PARKER IN A REVIEW OF "LIGHT AND THE
BEHAVIOR OF ORGANISMS"

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In this journal, Vol. 1, pp. 461-464, there appeared a review by G. H. Parker of the book entitled "Light and the Behavior of Organisms." Certain statements in this review seem to indicate that the position of the author of the book, the present writer, was not grasped, other statements show clearly that the author of the review takes exception to the interpretation of various phenomena as described by the author of the book. The questions at issue may be conveniently taken up *seriatim*.

1. Parker says, p. 461, "The facts, new and old, are marshalled with great consistency and uniformity in support of Jennings's well-known views on animal orientation, and this method of presentation is often so vigorously pursued as to give the reader the impression of special pleading rather than sound judgment. Many of the cases chosen to illustrate the 'trial and error' method of orientation must strike the impartial reader as equally good examples for the support of the 'tropism' theory." I do not understand how my reviewer came to the conclusion that cases were chosen to illustrate the "trial and error theory" or any other theory of orientation. I reviewed practically all previous work on orientation and thoroughly investigated the subject myself, studying the process in representative species of plants and of all of the different classes of animals. The methods of orientation in all are described in detail regardless of what theories they fit. Judging from Parker's statement one might conclude that all had been discarded except those which fit preconceived notions. Whether or not "sound judgment" was exercised in dealing with the subjects treated is a question which I shall leave in the hands of my readers.

2. Parker implies repeatedly in his review that the methods of orientation as described in my book support "the tropism theory." But unfortunately he fails to state which one of the fifteen¹ different tropism theories presented in my book, pp.

¹ There are now seventeen, two new ones having recently appeared.

53-55, he considers as "the tropism theory," and without such a statement his criticism is meaningless, for every method of orientation described is in accord with one or another of the fifteen theories presented. They are practically all tropisms in one sense or another and I have nowhere even so much as intimated that they are not. I have however pointed out in many instances that various methods of orientation do not support certain prominent tropism theories. I am greatly disappointed that my critic has used this term in such a loose way after all the time and energy I spent in trying to show what endless confusion has been caused by just such carelessness.

In answer to two letters addressed to Professor Parker requesting first, a definition of the term tropism and second an explanation of its meaning as used in his criticism he says in his first reply: "I frankly confess that I cannot give a clear definition of the tropism theory or the theory of trial and error"; and in his second: "The gist of the tropism idea as it lies in my mind is that it is an orientation reaction dependent upon unequal stimulation of two symmetrical parts of the organism's body."²

Since Parker admits that he cannot define clearly either the tropism or the trial and error theory it is not surprising that he concludes, as quoted above, that certain cases which illustrate the one serve equally well to support the other: Hazy definitions invariably lead to confused thinking. I may add however that I have had no difficulty in understanding what Jennings means by trial and error, and I assume that this is what my critic implies by the "theory of trial and error."

3. In the process of readjustment to a change in the direction of illumination, Stentor may either stop and turn abruptly or it may turn gradually. In the gradual turning from the source of light Parker says we have a "good instance of tropic response." This conclusion like the one referred to above is not surprising on the basis of a tropism theory that cannot be defined clearly. But let us apply the definition Parker furnished in his second letter and see what ground there is for it. By referring to this definition quoted above it will be seen at once that it can be applied strictly only to bilaterally or radially

² In a later communication Parker requests that it be made clear that in his first reply he refers to a definition which would be acceptable to a majority of those using the term, and that in his second reply he gives a personal definition.

symmetrical organisms since only such have "two symmetrical parts." Stentor is neither radially nor bilaterally symmetrical and consequently strictly speaking none of its reactions can fit Parker's definition of tropisms. Even if we interpret this definition very liberally and substitute opposite sides in place of symmetrical parts there is no evidence that the gradual turning of Stentor from the light is tropic as Parker maintains, for it responds only when, in the process of turning the light intensity on the oral side is increased, not when other surfaces become more strongly illuminated. This I have fully described in the text as well as in the legend, Fig. 14, p. 117. In spite of much time and energy spent I was unable to obtain any evidence whatsoever indicating that any reactions in Stentor are dependent upon unequal stimulation of opposite sides, pp. 114-115. It is consequently evident that as far as my experiments and observations are concerned there is no evidence whatever indicating that any features in the process of orientation in Stentor are "tropic" in accord with Parker's definition of this term.

4. It is maintained by my critic that I have not "made clear how an organism, after it has once become oriented, can continue to move in a straight line without involving the essential elements of the tropism theory." I assume that in this connection he means by "essential elements of the tropism theory" reactions due to equal "stimulation of symmetrical parts of the body. If my description of the process of orientation in *Euglena*, pp. 92-97, Stentor, pp. 114-119, fly larvae, pp. 189-193, and a number of other organisms is understood it will be clear without further elucidation how organisms can take a fairly straight course without equal stimulation of symmetrical parts. (The idea that organisms move in a "straight line" is more imaginary than real.) I have stated my position regarding this matter referring to *Euglena* (p. 230) briefly but clearly as follows: "The reactions caused by changes of intensity result in directing the organisms toward various points of the compass. As soon as they reach a position in which the rotation on the long axis no longer causes a change of intensity on the sensitive region there is no longer any cause for turning; they therefore continue in this direction."

According to this explanation the organism retains a given direction of locomotion not because of continuous action of light,

but because it tends to move in a direct course in the absence of external stimuli. Thus we find that earthworms, e. g., oriented in light, continue in a given direction for some distance after the light is entirely cut off. The most striking demonstration of this is seen in fire-flies in which the orienting stimulus consists of a flash of light. Orientation and movement toward the place where the flash occurred takes place in darkness. Here then there is no possibility of light acting continuously in directing the animal on its course. Why should it be necessary in other forms as Parker assumes?

5. "But the chief general defect of the volume," says Parker, "is one that has been inherited from earlier students in this field of work, and consists in the attempt to apply the trial and error method of orientation to the movements of many of the higher invertebrates, such as the earthworm, fly larvae, etc., to the exclusion of the tropism idea." He then singles out the reaction of the earthworm for special criticism with reference to this point. On the basis of his own definition previously quoted have we in reality attempted to apply "the trial and error theory . . . to the exclusion of the tropism idea?" On page 200 we find the following sentence: "If the [earthworm] however is rather sluggish so that there is little lateral movement of the anterior end it turns from the source of light with very few exceptions" (very few trials). On the same page there is a table which shows that out of 90 exposures to unilateral illumination the specimens used turned directly from the light 80 times and toward it only 10 times (scarcely any indication of trial). And again at the bottom of the page I have made the following statement: "In a few other sluggish specimens the exposure to unilateral illumination was not made until after they had come to rest in light of 15 candle meters. Under such conditions the animals did not react at all until a few moments after the exposure, then they very slowly extended and turned the interior end from the source of light every time. . . . There was no evidence of even the slightest preliminary turning toward the source of light" (no trials whatever). After stating that trial reactions may function in the orientation of the earthworm I wrote, p. 204: "This does not indicate that constant light cannot also produce orienting stimulations." That is, it does not indicate that there are no tropisms even in accord

with Loeb's definition. And finally in the summary, p. 205, we find the following: "Under certain conditions, if one side is illuminated, they [earthworms] always turn toward the shaded side without preliminary movements and therefore orient directly" (no trials). Can it be possible that my critic actually read the section of my book containing the quotation given above and still came to the conclusion that I have "attempted to apply the trial and error theory . . . to the exclusion of the tropism idea," assuming that he meant by the "tropism idea" merely orientation without trial movements. The truth of the matter is that no attempt was made to apply any theory whatsoever, but there was a very serious attempt made to describe precisely how orientation occurs in all of the different forms studied. In the fly larvae it is true I found no evidence of direct orientation, no reactions in accord with Parker's definition of tropism. But by merely glancing over the general summary, pp. 228-235, it will be seen that according to my conclusions, direct orientation, i. e. orientation without trial is found in coelenterates, earthworms, planaria, mollusks, arthropods, and vertebrates. Note the following statement found on page 233: "mollusks, arthropods and vertebrates all orient directly. There is little evidence of preliminary trial movements in this process in these forms." Do not these statements show that if there was an attempt made to apply trial reactions to the exclusion of other factors in explaining orientation the attempt must have been a miserable failure?

Orientation is unquestionably direct in many instances, i. e., without trial and in accord with Parker's definition of tropisms, provided he includes under the phrase "unequal stimulation of symmetrical parts," cases in which the stimulus may be confined to either side, it being zero on the opposite side; which would in reality mean that orientation may be due to a differential response to localised stimulation. If however he means to imply in his definition that both sides of the organism are continuously unequally stimulated during the process of orientation and continuously equally stimulated after orientation in accord with Loeb's last theory of tropisms, I have no conclusive evidence in support of his "tropism idea."

6. In discussing the efficiency of trial in the process of orientation Parker bases his argument upon a hypothetical case. Assum-

ing that an earthworm becomes oriented after making five preliminary trial movements, he says, p. 463: "In this total act the significant part so far as ultimate orientation is concerned is not the making of the five trial and error movements but the final 'selection' of the best one as a line to be followed in the real locomotor act. Now it is difficult for the reviewer to see how this 'selection' can be accomplished without involving just that feature of symmetrical stimulation which is the essential part of the tropism idea. The worm presumably moves finally in the direction of that trial which through the stimulation of symmetrical points on its body has been found to be most favorable for orientation. Without complicating this problem by raising the question as to the means by which the worm could retain impressions of the five trial and error movements preparatory to following up one of them, it must be evident that these movements in their effect on orientation are quite subordinate to symmetrical stimulation, in fact, not essentially involved in orientation at all."

What necessity is there for assuming "symmetrical stimulation" and "retention of impressions" of preceding movements in the process of orientation by trial? Contrary to Parker's implication I did not emphasise trial as a factor of exceptional importance in the orientation of the earthworm and I referred to it only very briefly. But I did discuss this question rather fully in my description of the process of orientation in fly larvae, pp. 189-196. Careful reading of this description will convince almost any one that there is no necessity whatever of assuming "symmetrical stimulation" or "retention of impressions" to account for orientation by trial reactions. Not only is this true in the case of fly larvae but there is good experimental evidence for opposing especially the former assumption. This evidence is found on pages 194 and 195 with the following conclusion: "The orienting reactions [of fly larvae] could readily be explained by assuming the area sensitive to light to be restricted to a small mass of substance located in the middle of the very tip of the anterior end."

But my reviewer is not the only one who seems to have difficulty in understanding how orientation by trial could occur without the activity of psychic factors, to say nothing about mystical factors of various sorts. Witness e. g. the statements

of Bohn and Loeb in all of their recent papers referring to this subject. And this in spite of the fact that in the numerous descriptions of orientation by this method given by Jennings and myself no such factors whatever are involved or implied.

The main difficulty these authors have in grasping the subject lies in their assumption that locomotion is dependent upon the same factors which regulate the direction of locomotion, an assumption for which, as far as I am aware, there is absolutely no evidence.

Let us attempt to clear up these matters by means of an illustration: Suppose an active blind fish be put into an enclosure with a small opening at one side leading into a long narrow straight passage. The fish swims about, strikes the wall of the enclosure, turns and takes another course, strikes the wall again, then proceeds in a different direction, etc., until finally it strikes the opening and enters the narrow passage. The fish has become oriented and if there is nothing to turn it out of its course it may proceed through the passage without further stimulation, but if it is turned out of its course it strikes the wall of the passage, turns and soon becomes oriented again. Surely no one will maintain that it is necessary to assume "symmetrical stimulation" and "retention of impressions" of the various movements in order to account for the orientation of the fish. And what basis is there for the assumption of psychic factors! It would indeed be a comparatively simple task to construct a machine with wheels and springs and levers so arranged that after striking an obstacle it would back off and take a different course, and if put into an enclosure similar to that assumed in case of the fish it would finally strike the opening and become oriented. As far as trial movements are involved in the orientation of fly larvae or earthworms the process is, in principle, precisely like this. The organism just like the hypothetical machine or the blind fish in the enclosure continues to turn in different directions assuming different axial positions until the stimulus which causes the turning ceases. And the same principle is involved in every account of orientation by trial in the lower organisms that has been given either by Professor Jennings or myself. Note, e. g., the following statement from Jennings quoted in my book, p. 47: "[The so called trial and error method of orientation] consists in successively 'trying' not only different directions of locomotion

tion, but also different positions of the body axis. As soon therefore as a position is reached in which the disturbance causing the reaction no longer exists, the reaction of course stops; the animal therefore retains this axial position."

I am unable to understand how my critic could have read this statement and the account I have given of orientation by the trial method in fly larvae and various other forms and still maintain that "symmetrical stimulation" and "retention of impressions" is necessary to account for the process observed and described.

7. Professor Parker implies that there is serious confusion in the sequence of authors' names throughout the entire volume. He writes, p. 463: "It is difficult to understand the ground for the sequence of authors' names such as occurs in the categorical statement made on pages 265 and 266, where, contrary to the common practice, the order of dates is not followed. This looseness at times comes to be really misleading where, for instance on page 52, Verworn precedes Loeb with dates 1886 and 1887, while in the bibliography Loeb's earliest reference is given with the date 1888, and Verworn's with that of 1889." The looseness referred to in this statement is more imaginary than real as any one interested can ascertain for himself. As a matter of fact the criticism would not call for a reply if it did not bring up the question of priority between Loeb and Verworn.

The sentence containing the dates to which Parker refers in this connection reads as follows: "The study of animal behavior from the physico-chemical point of view was first taken up by Verworn and Loeb in 1886 and 1887." The dates found here clearly have nothing to do with dates of publications recorded in the bibliography, and I can see no reason why they should be misleading, especially since, in referring to the investigations of Verworn on the activities of protozoa, I stated, p. 6, that "these were taken up in 1886, two years before Loeb's first preliminary note on the reactions of animals appeared." I did not go into the matter further because I was not primarily interested in the question of priority concerning the authors in question. In all probability each of them began work on animal behavior from a purely objective point of view independent of the other. The facts concerning this matter are as follows. In 1889 Verworn published a paper entitled *Psycho-physiologische*

Protisten Studien" covering 218 pages. In this he describes in detail the reactions of a number of animals and discusses them from a physico-chemical point of view. In the preface it is stated that he began the work in 1886 just as I stated in my account.

Loeb's first paper dealing with behavior appeared in 1888, under the title "Die Orientierung der Thiere gegen das Licht. (Thierischer Heliotropismus)." It is a sort of preliminary report consisting of but five pages published in the proceedings of a medical society at Würzburg. A much longer paper with a similar title appeared later in pamphlet form. This pamphlet is dated 1890 indicating that it was published during the year following the date of publication of Verworn's paper. Loeb, however, usually gives the date 1889 in referring to this paper (see *Studies in General Physiology and Dynamics of Living Matter*) thus intimating that it was not preceded by Verworn's paper. Why he gives an earlier date than that found on the pamphlet I am unable to say.

These are all of the important facts at my command concerning the dates of the earlier works of these authors. Those interested in the question of priority may use them as they see fit in drawing their conclusions. However in discussing priority of work on the behavior of organisms from the mechanical point of view the brilliant investigations of Engelmann beginning as early as 1869 must not be overlooked.

NOTES

PECULIAR ACTIONS OF A STRIPED GROUND SQUIRREL

ROBERT B. ROCKWELL

Denver, Colorado

Glimpses of the inner nature of wild creatures are encountered by observers at the most unexpected times and places, and such an experience fell to the writer's good fortune early last June.

Some fifteen miles northwest of Denver, Colorado, is a small



lake leased by a number of Denver men for duck shooting. The so-called "club house" is a frame structure of one room, which serves the manifold purpose of kitchen, sleeping room, store room, etc. It is occupied but one night during the week for only a few weeks in the spring and fall and is overrun with house mice. The shooting season closed April 15th, and the house was not again occupied until the night of June 3d. On this evening the writer, with a companion, reached the cabin some time after dark, and preparations were made to retire.

In the corner of the cabin was a pile of three folding spring

cots, and on top of these was a camp mattress. The cots and mattress were taken out of doors and set up (for we were outdoor sleepers) and the writer promptly turned in. I had no sooner become quiet than I heard a chorus of tiny squeaks coming from inside the mattress, and an examination revealed a warm nest in the padding containing eight tiny, naked, blind creatures whose eyes were not yet opened. Supposing them to be young mice they were ruthlessly disposed of, as mice usually are, and I prepared to resume my slumbers.

I was aroused a few minutes later by my friend (who had not yet retired) calling me softly to hurry into the cabin, and once there a sight met my eyes that I will long remember.

Under where the cots had been piled was a knothole in the floor; this, however was not directly under the position of the nest, which was rather toward one side of the mattress but more to the other side of the space which had been covered by the cots and both were well toward one end of the latter. Emerging from this hole was the mother of the little ones we had just assassinated, but instead of a mouse, it proved to be a large, handsome Pale Striped Ground Squirrel (*Citellus tridecemlineatus pallidus*). As this species is, to the best of my knowledge, strictly diurnal, and the time was between 10 and 11 P. M., it seems very probable that the animal had been frightened from the nest by our entrance and was now returning.

Upon reaching the floor she seemed greatly confused, but after some hesitation she ran to the place from which she had probably been in the habit of climbing up the frames of the cots to the nest. Here she stood upon her hind legs and frantically pawed the air, apparently trying to locate the missing frames. Then she ran back to the hole and repeated the entire performance. She would stand straight up on her hind legs, as straight as a man could stand, and after turning round and round, would fall backward, only to jump up and run about in various sized circles in a vain endeavor to locate her missing family. This performance was continued without a pause for fully fifteen minutes, during which time her excitement and confusion visibly increased, and although we were both within arm's length of her and spoke frequently in an undertone, she did not pay the slightest attention to us. Several times she jumped high in the air from a standing position and falling

to clutch the accustomed frame would fall backward, after which she would spin around repeatedly much after the fashion of a wounded creature. She did this always from practically the same spot. During the latter part of the performance she continually gave utterance to low cries and moans, and her entire manner gave the plainest evidence of grief and excitement. In all my experience with wild creatures, I have never witnessed a more keenly pathetic scene.

Finally, after we had satisfied ourselves that further observations would reveal nothing new, we decided to capture her and photograph her the following morning (it was by this time almost midnight), and here we received a great surprise, for, although she eluded our hands and in doing so exhibited wonderful strength for so small an animal, she did so in a half-hearted manner, and although the knothole was within a few feet, she did not attempt to escape by that means except once, and even then she was back going through her queer performance within a minute.

Previous experience with these little creatures had taught me a wholesome respect for their sharp teeth, so we approached her with heavy gloves, but even when we held her tightly in our hands she exhibited neither fear or anger, and instead of biting fiercely as is usual with this species, she simply nibbled feebly at the gloved finger much as a house cat might scratch at a door it wanted opened.

After capturing the animal three times and allowing her to escape each time for fear of injuring her in her struggles, she was finally placed in a box and we retired for the night. The next morning we made a narrow box with glass sides and no bottom and prepared to make a series of studies. She was somewhat wilder in the sunlight and became quite panic stricken when first put into the glass box, the glass sides being altogether beyond her comprehension; but after a few minutes she quieted down and a highly interesting series of photographs was the result, one of which published herewith shows the erect position above described.

After half a dozen exposures had been made the captive was liberated and promptly scampered into the nearest burrow, and since that time we seldom visited the "club" during the long summer and fall without being greeted by her sharp, clear

whistle, though she took particular pains to keep far away from our inquisitive fingers.

COMMENTS ON MR. ROCKWELL'S OBSERVATIONS

By EDWARD R. WARREN

Colorado Springs, Colorado

The preceding notes were written by Mr. Rockwell at my request after he had told me about the occurrence in conversation, as it seemed so interesting as to be worthy of record.

The animal seems to have been unable to realize that the cots, which had not only supported the mattress in which the nest was, but also covered the hole in the floor by which she had entered the room, were missing. One would think she would have noticed their absence at once, as heretofore they had been there when she went to and fro. It is possible that being a diurnal animal, her confusion may have been due to being disturbed in the night, and that she was even unable to see well by such light as my friend may have had there, though this last would not account for her actions. It is an interesting speculation as to whether she would have acted as she did if it had been daylight.

DELAYED IMITATION IN A CAT

EDWARD R. WARREN
Colorado Springs, Colorado

The two cats whose behavior is described in the following notes were own brothers, of the same litter, born in July, 1898, on a ranch near Crested Butte, Gunnison county, Colorado. As they were named, I shall refer to them hereafter by their names, "Tom" and "Snowball." The former was a large-boned yellow and white cat, never very fleshy, the latter a chunky, black animal, apparently smaller, but weighing nearly as much as Tom. Both were castrated when eight or nine months old. The winter of 1898-9 spent at the ranch with the son of the owner, with the cats for company. Just how it came about I do not remember, but Tom learned the trick of coming up on my lap when I was sitting in a chair, thence to my shoulder and on my outstretched arm and taking meat held on a fork. Sometimes he would do it if I was standing up. Snowball would never do this.

I left the ranch the spring of 1899, but remained in the vicinity and frequently visited there until late in the fall of 1902. Whenever there at a meal, and that was quite often, I usually fed Tom in this way for amusement, but none of the members of my friend's family ever troubled themselves with it. Snowball was invariably on hand at mealtimes, and his appetite was as good as his brother's, but, though I used to talk to him and coax him, he would never come up after the meat. His "stunt" was to pull the meat from the fork with his paw and convey it to his mouth that way, but only when he could reach the fork from the floor.

I was absent the winter of 1902-3, returning for a short time in July, 1903, and Tom came up for the meat readily at the first offer, and Snowball, as previously, refused. From July, 1903, to October, 1905, I did not see the cats, but the last mentioned date made another visit, and as in 1903, Tom showed he had not forgotten, and scrambled up at once when invited, while Snowball did not.

Then came a still longer interval, until January, 1909, before

I returned for a visit. The cats were active and lively, and it will be noted, were in their eleventh year. I asked my friends if anyone had fed Tom in my way since I had been there last, and they said no one had done so. So I had much curiosity to see if he would remember, as it was now over three years since I was there last. Sitting in a chair and taking a bit of meat on a fork and holding it out at arm's length (out to one side, not in front), I spoke to Tom and told him to come up if he wanted it. He looked at me and at the meat, and seemed puzzled; I continued talking to him and then he apparently remembered, but imperfectly or doubtfully, for, instead of coming up with a rush as had been his former habit, this first time he climbed up rather deliberately and hesitatingly and took the meat. But only the first time did he hesitate; after that he wasted no time. Snowball was, of course, present while this was going on. Unfortunately I kept no notes of the matter, so cannot say if it was the first time or a meal or a day or two after that the surprising thing took place. Tom had taken a piece of meat from the fork and jumped to the floor to eat it and I was holding out more, talking to Snowball, who was begging for it, telling him it was his for the taking, and apparently he decided he could do what his brother did, for suddenly he came with a scramble to my shoulder and secured the tidbit.

To say I was surprised puts it mildly, for I looked for nothing of the sort after all those years and was merely teasing him as I always did. I had always given him his share in his own way. I remained nearly two weeks, and during the remainder of the time Snowball vied with Tom in taking the meat, often there was a race up on my lap for it. There was another cat at the ranch (and it was not a cat ranch!) a half brother of these two, nine months younger, "Sunflower" by name, or "Sunny," for short, a large yellow animal. His appetite was as good as the others, but he would not climb for his food, so went without to some extent. I do not wish anyone to infer that feeding from the fork was the only way those cats were fed, for they had plenty to eat besides, and were out about much after mice. The feeding with the fork was simply done for amusement.

It is certainly very strange that Snowball should have waited so long before learning his brother's trick or imitating him, however it may be best expressed, when he had seen it done

so many times before. If he had not seen it frequently done, it would not be so odd, but it can be said, with little or no exaggeration that he was present every time Tom got a bit of meat in that fashion, and, moreover, as I have said before, I always talked to him and coaxed him to take the same way also. It was not due to any stupidity on his part, I think, for he always seemed as bright, smart and active as his brother, in fact he seemed quicker in some ways. I make no pretense of being a psychologist, and will leave it to those who are, to explain this behavior. I have stated the facts as clearly and correctly as I could.

PSYCHOLOGICAL RESULTS IN REACTIONS TO TONE BEFORE AND AFTER EXTIRPATION OF THE TEMPORAL LOBES.

WALTER B. SWIFT, M. D., Boston

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From the laboratory of Professor L. Jacobsohn, Berlin, Germany.

A German court dog, Louisa, was trained to take meat at a low tone (eating tone of Kalisher) and refrain from taking it at a high one. Then his left temporal lobe was removed by Prof. L. Jacobsohn in Berlin. After three days' rest, the same training was continued, and when good response was re-established, the right temporal lobe was removed by him. Training was resumed by me.

I give here merely an epitome of the psychological results of the training and operations. The normal dog under my training took about fourteen days to learn to react correctly and eat at the low tone and refrain at the high tone. At first he grabbed at the food indiscriminately, tone or no tone, then (after severe punishment), when the high tone was sounded, gradually learned to refrain at the high tone for fear of punishment. After two weeks of such discipline, one could easily see that the dog had some clear idea that he must refrain at one tone and eat at the other. During a month of such training, gradual improvement resulted so that reaction was quicker, more exact; more being mistakes were corrected. I found at first he was inclined to react to motion rather than sound, and watched me closely for the motion accompanying the low tone, and would react to that. Too little food resulted in an eagerness to eat, and made many failures, and too much food brought a refusal to act at all. When this trick was well learned, he was operated on as above, and after three days' rest, training was resumed by me; and at the first test, he reacted correctly and ate at the low tone. But reaction came now decidedly slower than before, and never up to the second operation regained quite the exactness and quickness that the dog showed before any operation was performed. A gradual increase was, however, noticed in these qualities of execution. After many days had passed, during which best results possible

were obtained, the right temporal lobe was removed, and the dog, without any temporal lobes, was trained again as before. And now appears the result that surprises the student of brain localization.

After a period of training, lasting two weeks with no sure response to sound—very gradually the ability to differentiate the high tone from the low one returned. Slowness and almost an ataxia in the head movement with an occasional false act characterized the whole period of reactions after the second operation. But it was plain, as was testified by some eminent scientists who came to see the dog in the laboratory in Berlin, by the members of the German Neurological Society before whom I demonstrated him, and also in this country, by the Boston Neurological Society, and other scientists, including Prof. Yerkes, who saw the dog at my home in Boston—it was, I say, plain to all these men that the dog reacted to a sound stimulus and differentiated two tones when both temporal lobes had been extirpated. Prof. Yerkes pronounced him acutely sensitive to sound, and suggested that I try to teach him a set of new associations, so I tried making him get up to a chair placed before him to reach the meat, rather than bob his head downward for the meat on a block below him. This met with success for even in only a few trials, the dog shot his head upward for the meat at the eating tone, when before he had dropped it directly downward. This too, when a blast of air was introduced to eliminate smell as a guiding agent in directing the reactions.

For a more exhaustive report of methods, technique, macroscopical and microscopical findings, the reader is referred to the report of a paper read in Berlin before the *Gesellschaft für Psychiatrie und Neurologie* in the *Neurologisches Centralblatt*, November 13, 1910, and to the *Journal of Nervous and Mental Disease*.

The autopsy findings, i.e., the macroscopic appearance of the area where the brain substance was extirpated, show a total extirpation of both temporal lobes. (Only the microscopic findings to appear later can add further data.)

These results lend weight to Kalischer's findings, although we offer a different interpretation. Kalischer claimed that the association process of tone differentiation was a mere reflex

located in the basal ganglia and like other mere reflexes, as the Achilles reflex and the knee jerk (exclusive of its cerebral element), had only a peripheral activity consisting in an afferent impulse with a ganglionic transfer of motion into a motor impulse passing over an efferent nerve with absolutely no cortical relation whatever. Rothman, failing to obtain any positive results in tone differentiation, concluded he had extirpated the cortical area subserving that function. The conclusions of Prof. Jacobsohn and the writer place the functions in an entirely different location from either the basal ganglia or the extirpated temporal lobe.

We locate the differentiation of tone in the cortex ex-temporal. My reasons for this cortical localization are the presence of psychological elements in the execution of the act which differentiates the execution from that of a mere reflex. These psychological elements are *purposefulness*, *slowness*, *inhibition*, and the need always to *relearn* the execution of the constellation of inter-related perceptions and executions.

To take these up briefly in detail:

(1) A mere reflex is always quick—blitzartig as the Germans say—it shoots the determined act off “too quick for thought.” The eye reflex, various protective reflexes, and in the neurological field the corneal, cremaster, and the knee jerk, recall the quickness of the motor response to stimuli. In contradistinction, the act of Louisa to tone had a noticeable ever present *slowness* about it. This alone to me would be pathognomonic of a premeditated cortical act.

(2) Then *inhibition* is another quality that is foreign to the mere reflex. The constant waiting and watchfulness to listen and differentiate the tones and the persistent prevention of motor action at the wrong time shows the inhibition in its cerebral sense was a pretty constant factor in the behavior of my dog Louisa.

(3) All know that mere reflexes are without sustained purposes and surely the eating act to tone stimulus had an ever present *purpose*.

(4) Mere reflexes are never learned, never have to be *re-learned*, never are forgotten and have to be recalled to memory. All of these elements—qualities of cortical function—were pres-

ent at one time or another during the one and a half years of training to which I subjected my dog.

Therefore I concluded that the location of the act was in the cortex somewhere outside of the extirpated temporal lobe.

To sum up: A dog may be trained to differentiate two tones; and after extirpation of both temporal lobes, has ability to react differently to different tones, and can be taught new associations.